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TRANSACTIONS

OF THE

ENTOMOLOGICAL SOCIETY

OF LONDON

Vol. 79. 1931.

INSECTS AND CLIMATE

By B. P. Uvarov

(Senior Assistant, Imperial Institute of Entomology).

With a Prefatory Note

By Captain A. F. Hemming, C.B.E.

(Joint Secretary, Economic Advisory Council).

[Read November 5th, 1930.]

In December 1928, the Society published in its *Transactions* (*Trans. Ent. Soc. Lond.*, **76** : 255–343) a paper on insect nutrition and metabolism by Mr. B. P. Uvarov. This paper was prepared at the request of the Dietetics Committee of the Committee of Civil Research, and its publication was financed by a grant from the Empire Marketing Board. The Dietetics Committee of the Committee of Civil Research (which in January 1930 was absorbed by the Economic Advisory Council) is constituted as follows :—

Major Walter Elliot, M.C., M.P. (*Chairman*).
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Dr. A. T. Stanton, F.R.C.P., D.P.H., Chief Medical Adviser, Colonial Office;
Captain A. F. Hemming, C.B.E., Joint Secretary to the Economic Advisory Council (*Secretary to the Committee*).

Some months after the publication of Mr. Uvarov's paper, the Dietetics Committee, in consultation with the Ministry of Agriculture and Fisheries, invited the Empire Marketing Board to provide funds for a survey of insects in relation to climate. This suggestion was prompted by the fact that arrangements had been made for a meeting in August of that year of the Imperial Meteorological Conference. The Empire Marketing Board approved this proposal and Mr. Uvarov was invited to undertake this important work.

As will be seen from Mr. Uvarov's Introductory Note to this paper, the task of summarising the literature on insects and climate proved to be more formidable than was originally anticipated. It was for this reason that it was not until August 1930 that Mr. Uvarov was able to submit his results to the Dietetics Committee of the Economic Advisory Council.

On the recommendation of the Dietetics Committee, the Empire Marketing Board offered this important paper to the Society for publication in their *Transactions* and accompanied that suggestion with an offer to contribute the greater part of the cost of its publication. This offer was gratefully accepted by the Society, which undertook to publish Mr. Uvarov's paper as a separate part of their *Transactions* for the year 1931. It is thus due to the financial support accorded by the Empire Marketing Board that the preparation by Mr. Uvarov of this valuable contribution to economic entomology and its publication in the *Transactions* have been rendered possible.

Arrangements were also made between the Society and the Empire Marketing Board for the supply to the Economic Advisory Council of a limited number of separate copies of Mr. Uvarov's paper for distribution at the discretion of the Council.

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INTRODUCTION.

Economic entomologists of the present day are no longer satisfied with merely recording the outbreaks of insect pests and with devising means for their control. They realise more and more that their chief aim and highest ambition must be to foresee and to prevent outbreaks. In order that they may be able to do this, all conditions accompanying and causing outbreaks must be thoroughly investigated and elucidated; in other words, the epidemiology of insect pests must be the central problem of economic entomological research, which should be carried out from the ecological point of view. The ecological conception of economic entomology consists in the recognition of the injurious insect as an integral part, and even as a product, of its environment.

The environments of different insects vary to an enormous extent, but there is one group of environmental factors, from which there is no escape for any terrestrial insect. These are the temperature, humidity and other conditions of the habitat, which may be classed as almost entirely meteorological in character. It would be a mistake to believe that meteorological conditions can affect only those insects which are exposed to the direct action of the atmosphere, since the conditions of the temperature, humidity, etc., in the soil, or inside a tree-trunk, or in any other habitat, are closely dependent on the intensity of the solar heat, on the amount of precipitation, on the humidity and evaporating power of the air, in fact on the whole complex of phenomena covered by the word climate.

Climate, then, is the ever-present factor in insect life. This does not necessarily mean that it is always the factor on which the existence of an insect entirely depends, but the other conditions of the environment are subordinate to it in importance. The relative value of all environmental factors is not the same for all cases and only detailed ecological investigations throughout the life-cycle of an insect make it possible to evaluate the factors. However, even in those cases where the existence of an insect depends to a greater extent on conditions other than climatic (for example on the presence of its food-plant), climate still remains as a definite, if not dominant, factor.

These considerations lead inevitably to the conclusion that any studies on a living insect must begin with the investigations of its climatic environment. This conclusion is, of course, far from being original, as is evidenced by the existence of an enormous literature on the influence of climatic factors on insects. This literature, however, is very scattered, and so far no attempt has been made to take stock of it, in order to see what is already known, and what remains to be studied. The present summary was started with this end in view, and is intended mainly as a basis for practical bioclimatic studies on economic insects. Climate, however, is an extremely intricate complex of phenomena, and it is hopeless to attempt to study its influence on insect life by methods other than analytical. Each separate factor of the climatic environment should be studied by itself, and its effects on each phase of the insect's life should be investigated independently.

This work belongs to the field of experimental physiology, which studies the responses of an organism to the controlled degrees of each isolated factor. Accordingly, the first part of this summary deals with the data obtained by investigators of insect physiology, and is intended to serve as a theoretical foundation for the second part, which contains a survey of the facts relating to the influence on insects of the climatic environment as it exists in nature. Many entomologists would be inclined to suggest that the latter is the only kind of data that can be of any practical value, while the investigations under experimental conditions have a very remote relation to the actual course of events under natural conditions. It will be seen from the summary that this view is erroneous, since most of the problems of distribution, development, and of the activities and abundance of insects can be attacked only on the basis of a thorough understanding of the physiological processes involved. The physiological research, carried out in a laboratory, is a basis for the practical studies in the field.

From this point of view, physiological investigations on an insect should, in their turn, not be regarded as an end in themselves, but should be planned and carried out in such a way that the results can be utilised in field work. This means that the combinations of factors studied in experimental work should always be chosen with due regard to the conditions which an insect is likely to encounter in nature. It is only by judicious correlation of experimental work with actual conditions, and of the practical conditions with the results obtained in a laboratory, that most of the problems of insect epidemiology can be elucidated, if not solved.

The task of summarising the literature on the subject proved to be much more formidable than was anticipated. About 1300 papers and books had to be examined; some of them were rejected, but over 1150, written in eleven languages, served as the basis for the summary. However, it cannot be claimed that the latter is exhaustive, since practically every paper on economic entomology contains some reference to the influence of climatic factors on the insect studied, but the inclusion of all such papers would be beyond practical possibility. It should be clearly understood, therefore, that the papers quoted in the second part of this work were chosen as suitable examples for the illustration of various points under discussion. These examples could be, in some cases, multiplied almost indefinitely, but this would only unnecessarily increase the bulk of the summary.

The work has been carried out under the auspices of the Empire Marketing Board, and it is a pleasant duty to express my gratitude to them for entrusting me with this very interesting task. I am very grateful to Captain A. F. Hemming, C.B.E., for the interest he has taken in the preparation and the publication of the paper, and particularly for the pains he has not spared in editing the typescript, a self-imposed and not an easy task. I am further indebted to Sir Guy A. K. Marshall, F.R.S., Director of the Imperial Institute of Entomology, for permission to undertake the work and for the facilities in carrying it out. My thanks are due also to Dr. S. A. Neave and Mr. F. J. Griffin for seeing the paper through the press. The librarian of the Imperial Institute of Entomology, Mr. C. J. Golledge, has greatly facilitated my work by his ready and competent assistance and I am very pleased to record here my obligation to him. Finally, I should like to thank a number of my colleagues, in this country and abroad, who have most willingly sent me separates of their papers dealing with the subject, supplied me with references, and helped in many other ways, thus showing their interest in this work and encouraging me in its execution.

PART I.

THE PHYSICAL FACTORS OF INSECT LIFE.

I. HEAT.

Physicists study heat phenomena from two points of view, since they make a distinction between the intensity and the quantity of heat energy, the first being expressed by the degrees of a thermometer, and the second by calories. Heat as an ecological factor should also be studied along these two separate lines, *i.e.* the influence on insects of various temperatures (high, low, fluctuating) should be studied apart from, or parallel with, investigations on the amount of heat energy, expressed in calories, necessary for the completion of a certain metabolic process, or sufficient to kill an insect. The quantitative side of the action of heat on insects has never been studied, or, at any rate, quantitative work has never been based on the evaluation of the amount of energy in the correct units, viz. calories. Instead, all investigators have considered only the temperatures, *i.e.* the intensity factor, and quantitative data have been obtained by taking into account the time during which a certain temperature has acted on the insect.

It is probable that estimations of heat energy in calories would prove too difficult with living insects, but this is a theoretical argument since, as stated above, no work has ever been attempted on these lines. We have, therefore, to summarise the available information on the influence of the intensity of heat, *i.e.* of temperatures, on various aspects of insect life.

All temperatures in the present work are expressed in degrees Centigrade.

(*a*) The Lower Fatal Limit.

The literature on the subject of the lower fatal limit of temperature and on the resistance of insects to cold is not inconsiderable, owing partly to the theoretical interest of the problem, and partly to its practical importance in the natural climatic control of hibernating insects.

Reaumur (1736) was apparently the first to investigate scientifically the fact that certain insects can be frozen so as to become hard and then revived again by raising the temperature; some caterpillars in his experiments survived a temperature of between — 9° and — 11° R. (— 7·2° and — 8·8°).

Later, the degree of cold resistance and the lower fatal limit was studied in a number of insects by various investigators. Some of the figures are presented in the following table (see Table I), which, however, does not include all the available data. (Apart from the papers quoted in the table, the following contain information on the subject: Antonov, 1922; Bachmetjew, 1899, 1900, 1900*a*, 1901, 1901*b*, 1902, 1907; Back and Cotton, 1924; Back and Pemberton, 1916, 1916*a*; Bacot, 1914; Baker and Turner, 1916; Bodenheimer, 1930; Feytaud, 1919*a*; Fischer, 1896; Frings, 1902–1905; Holmquist, 1928; Knight, 1922; Kyber, 1815; Lichtenstein, 1880; Loverdo, 1907; Ludwig, 1928; Lyman, 1892; Mell, 1922; Payne, 1926–1928; Picard, 1914; Pirsch, 1923; Plateau, 1872; Pouchet, 1866; Rahm, 1924; Reh, 1900; Reiff, 1910; Robinson, 1926–1928; Sacharov, 1928–1930; Shemigonov, 1902; Takahashi, 1913; Verson, 1871; Webster, 1899; monographs on economic insects often contain data on cold resistance and fatal limits, but no attempt had been made to compile the results.)

This table (Table I) demonstrates that there is not much uniformity with regard to the lower fatal limit of temperature in insects. Indeed, we see that certain insects may be killed by temperatures hardly below freezing point, but that others survive exposure to extremely low temperatures. Unfortunately the lowest figures available are not based on very exact experiments. The data by Spallanzani (1803) and Welter (1895) on the two moths surviving — 50° and — 40° respectively, are open to question. Of great interest are the observations made by Ross (1835) during the expedition in search of the North-West Passage. These were made on caterpillars of *Laria rossii*, Curtis, which after four successive exposures to the arctic frosts, varying between — 11·45° and — 47°, produced one adult moth and several parasitic flies.

(*b*) Theories of Cold Resistance.

As far back as 1709, Reaumur made his experiments on freezing some caterpillars and attempted to explain (1736) their resistance by the suggestion that in an insect, apparently completely frozen, there remain some fluids which freeze at a much lower temperature, and that death occurs only when all fluids are frozen. As we shall see later, this view, now two centuries old, was in principle correct. It is, indeed, much more so than the relatively recent theory of Bachmetjew, which for a long time was generally accepted, and which is repeated even by some modern authors.

Bachmetjew (1901, 1901*b*, 1902, 1902*a*, 1907) based his theory of cold resistance in insects on the observations of their body temperature by means of the thermoelectric method. These observations showed that an insect can be cooled gradually to a very low "critical point," which lies about — 10°. When this point is reached, the first crystals of ice appear in the tissues, and the body temperature suddenly rises a few degrees (see Fig. 1), to a point somewhat below freezing point. Further gradual lowering of the temperature causes the insect to become frozen quite hard. In this latent, or anabiotic, state no metabolic processes are possible, but the insect is not dead, and can be re-animated by warming. It is only when the insect is cooled to a certain "fatal point," which is at the same temperature level as the "critical point," that the insect is killed. The theory is, thus, based mainly on the purely physical conception

TABLE I.

EFFECTS OF EXTREME LOW TEMPERATURES ON INSECTS.

Insect.	Survived.		Killed.		Reference.
	Temp.	Ex-posure.	Temp.	Exposure.	
Orthoptera.					
Blatta orientalis			− 5	1 h.	Graber, 1887.
Blattela germanica	− 5	30 m.			Wille, 1920.
"Grasshoppers"	−30	30 m.			Walling, 1906.
Melanoplus mexicanus, eggs			−30	16 h.	Parker, 1929, 1930.
do. do. hoppers	− 7	24 h.	− 8	48 h.	
Coleoptera.					
Lema sp.			− 6	30 m.	Rödel, 1886.
Paederus riparius			− 4	45 m.	do.
Phytonomus sp.			−12	90 m.	do.
Sitophilus oryzae			−17·7	90 m.	Robinson, 1926.
do. do.			−12·2	3 h. 30 m.	do.
Sitophilus granaria			−17·7	2 h. 30 m.	do.
do. do.			−12·2	70 h.	do.
Bruchus obtectus			−10	3 h.	Carter, 1925.
Xylotrechus quadrupes, larvae and adults			− 1	3 m.	Boutan, 1907.
Melolontha melolontha			−12	1 h.	Faes & Staehelin, 1921, 1921*a*.
do. do.			− 8		do. 1923.
do. do. larvae			− 6		do. 1923.
Hymenoptera.					
Bees and ants			−15	3 h.	Dönhoff, 1872.
Apis mellifera			− 2·5	50 m.	Kozhevnikov, 1895–96.
do. do.			− 1·5	210 m.	Rödel, 1886.
Formica rufa			− 1·5	180 m.	do.
Rhynchota.					
Cimex lectularius, eggs	0	48 h.			Bacot, 1914*a*.
do. do. larvae	0	18 h.			do.
do. do. adults	−12·5				Pikel, 1898.
Lepidoptera.					
Cossus cossus, larvae			−21		Duval & Portier, 1922.
do. do. hibernating larvae	−20				Guyelard & Portier, 1916.
do. do. spring larva.			−17		do.
Nygmia phaeorrhoea, hibernating larvae			−15	7 h.	Grevillius, 1905.
Polychrosis viteana			−12		Hartzell, 1929.
Porthetria dispar, eggs			−19–20		Kulagin, 1897; Summers, 1922.
do. do. adult			− 4	30 m.	Rödel, 1886.
Ennomos spp., larvae and eggs			− 0·5		Merrifield, 1890.
Pyrameis cardui			−15	10 h.	Rödel, 1886.
Amorpha populi, larvae			−10	3 h. 30 m.	do.
Laria rossii, larvae	−47				Ross, 1835.
Macrothylacia rubi	−50	Several hours.			Spallanzani, 1803.
Bombyx mori	−40				Welter, 1895.
Diptera.					
Musca domestica			−12	5 m.	Rödel, 1886.
do. do.			− 8	20 m.	do.
do. do.			− 5	40 m.	do.
do. do.			− 6	3 h.	Dönhoff, 1872.
Piophila casei, larva			−15	64 h.	Simmons, 1927.
Anopheles maculipennis	−31	10 h.			Shtcherbakov, 1927.

of the supercooling of fluids. This is not surprising, since Bachmetjew was primarily a physicist.

Numerous experiments by Bachmetjew himself proved that the "critical point" depends on several conditions, *e.g.* (1) the velocity of cooling; (2) the stage of development of the insect and its sex; (3) the state of the insect whether starving or well fed; (4) the repetition of cooling; (5) the time of exposure, and (6) the "sap coefficient" (see below, p. 12).

Bachmetjew's theory was severely criticised soon after its appearance by a physicist, Kodis (1902), according to whom Bachmetjew had committed a series of technical errors in his work. According to this author, the supercooling of body fluids has nothing to do with the freezing of water in the protoplasm, with which the fatal effect of low temperature is connected. The criticism by Kodis escaped the notice of biologists, and Bachmetjew ignored it in his later works, in which he repeated and developed his views. More recently Maximov (1913) offered the following serious criticism of Bachmetjew's theory. By determining the quantity of ice formed in the pupae of *Celerio euphorbiae*, L., Bachmetjew found that all the fluids in them freeze completely at — 4·5°, while the critical point is — 10°; these figures seem to confirm the theory. However, the specific heat of the frozen pupae within the limits — 6·7° to — 16·3° was found by Bachmetjew to be 0·917, *i.e.* practically the same as that of the liquid fluids (1·01). The specific heat of ice is half that of water, and the same relation should exist between that of the frozen and the liquid body fluids. Since this was not the case, it may be assumed that the freezing process was incomplete at — 4·5°, and continued with further cooling. The inaccuracy of Bachmetjew's statement that body fluids freeze at — 4·5° is shown also by the fact that the blood of insects contains about 4% of salts, nearly 80% of which are sodium chloride. The eutectic point of sodium chloride solutions being about — 22°,

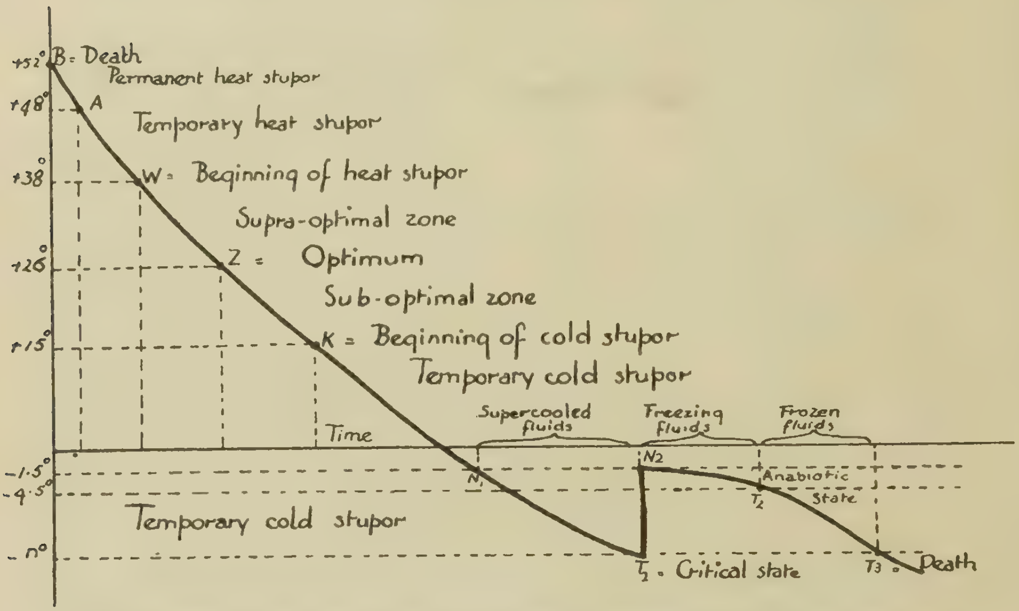

FIG. 1.—Zones of vitality and of death of an insect. (Re-drawn after Bachmetjew, 1907.)

the body fluids of an insect could not possibly freeze completely at — 4·5°, even if no other salts were present. Thus it seems reasonable to suggest that death from cold does not occur at a temperature considerably below that of the complete freezing of body fluids, as required by Bachmetjew's theory, but that, on the contrary, the fatal point is actually above that at which all body fluids become solid. This point of view has been confirmed in recent experiments by Sacharov (1928, 1930), who found that it was impossible to freeze completely the body fluids of insects even at — 21·2°, as in all cases some of the fluids remained unfrozen. Payne (1927*a*) found that complete freezing occurs only at a very low temperature, about — 40°.

The principal mistake committed by Bachmetjew consisted in his regarding the body fluids of an insect as a homogeneous liquid, following the relatively simple physical laws of supercooling and freezing. Actually, the body fluids, apart from a number of dissolved substances, contain a certain quantity of insoluble matter (particularly fat drops) and blood cells, the presence of which is bound to affect the physical properties of the fluids.

All these considerations lead to the conclusion that the theory of cold resistance elaborated by Bachmetjew must be abandoned. I have, however, considered it necessary to give this criticism of it somewhat fully as it is widely known and is still repeated in some modern text-books.

It is only quite recently that the problem of fatal freezing and of cold resistance has become better understood. Some of the old authors noticed that resistance to freezing is subject to individual variations in the same species; but Gueylard and Portier (1926) and Knight (1922) were the first to point out that there is also a seasonal variability in the cold resistance of insects. The two French authors observed that larvae of *Cossus cossus*, L., survived repeated freezing at — 20° in winter, but that the larvae of the same species taken in spring succumbed at — 17°. Knight's experiments were conducted with a Pentatomid bug, *Perillus bioculatus*, F. In winter it was possible to supercool the insects to — 17°, and, in one case, even to — 26° without actual freezing taking place, but in March and later in the season a temperature of — 10° was sufficient to cause freezing and death.

Very extensive and thorough studies on cold resistance in insects were undertaken recently by Payne (1926–1928). This author made numerous determinations of the supercooling and freezing points of various insects throughout their annual cycle. In the insects normally exposed to extreme temperatures, *e.g.* in various beetle larvae boring in oak, the degree of supercooling and freezing is clearly periodic, the greatest supercooling being found in winter and the least in summer. This is shown by the following figures.

	Outside temperature.	Supercooling point.	Freezing point.
February	—12·6	—22	—12·8
July	24	— 2	— 0·77

Insects infesting stored products, on the other hand, exhibited no periodicity but a considerable individual variation in the supercooling and freezing points. Thus, adult *Sitophilus granarius*, L., varied in their supercooling point from — 6° to — 14°, and in their freezing point from — 2·4° to — 8°.

It is natural to suggest that seasonal variations are connected with environmental conditions, particularly with the outside temperature. If this were the case, it should be possible to influence the degree of cold hardiness by artificial means. Payne has proved that this is so. In her experiments a preliminary exposure to a moderately low temperature caused a considerable lowering of the supercooling and of freezing points; *e.g.* in *Synchroa punctata*, Newm., the mean supercooling point is — 3·703°, the mean freezing point — 1·319°, but the individuals exposed for a week to — 3° acquired the supercooling point — 6·771°, and their freezing point became — 4·14°. Conversely, insects with a supercooling point of — 17° and a freezing point of — 12°, after being kept for two weeks at 29·4°, had the points raised to — 2·5° and — 1·4° respectively. A "hardening" of insects by gradual chilling, as described, cannot be, however, applied in all cases, but apparently only to the species normally exposed to winter frosts. In insects living under equable conditions, *e.g.* grain weevils, moderate lowering of the temperature for a long period only results in death (Robinson, 1926).

Apart from the seasonal variation in cold hardiness, there exist variations during the individual development of an insect. Ludwig (1928) studied the problem on the Japanese beetle, *Popillia japonica*, Newm., and found considerable difference in the ability to resist low temperatures between the larvae at different stages of development, their hardiness increasing at first, then decreasing to a minimum (just after the first moult). Hardiness increased considerably in the second-stage larva, which passes the winter under field conditions.

The question arises as to the reasons underlying specific, individual and seasonal variation in the cold hardiness of insects.

Bachmetjew (1901) paid attention to the fact that the supercooling and freezing points, as he understood them, are dependent on the "sap coefficient," or the percentage of liquid in the live weight of an insect. This coefficient is calculated from the formula $q = \frac{M - P}{M}$ where M is the total weight of the live insect and P its dry weight. The smaller the coefficient, the lower are the supercooling and the freezing points, *e.g.* in adults of *Aporia crataegi* :

Sap coefficient.	Supercooling point.	Freezing point.
0·56	−9·2	−1·4
0·58	−7·9	−0·9
0·61	−6·9	−0·8
0·62	−6·2	−0·7

Payne (1927*a*) found that cold hardiness can be induced by the partial dehydration of an insect. The following figures illustrate the results of the dehydration of larvae of *Synchroa punctata*, Newm., by placing them in calcium chloride desiccator at 15° :

	Supercooling point.	Freezing point.
Normal larvae . . .	— 6·7127	— 3·0412
Dehydrated larvae . .	—23·261	—11·481

Further, the same author discovered that cold resistance is increased by starvation, and decreased by abundant moist food.

These data suggest that cold hardiness is intimately connected with the total water content of the insect and with the amount of reserve substances. Sacharov (1928, 1930) arrived at these conclusions independently, and demonstrated in a series of interesting experiments the interrelations between the water and fat content of insects and the degree of cold hardiness. This author applied in his work not the thermoelectric method, but the dilatometer and criohydrates elaborated by Bouyoucos (1917), which permitted the estimation of the fatal temperature without injuring the insect by thermoelectric needles. That such injuries seriously affect the behaviour of the body fluids at freezing has been demonstrated by Carter (1925) and by Robinson (1928*c*), who has found that the injury raises the freezing point by several degrees.

Sacharov studied first the changes in the freezing point of the caterpillars of the brown-tail moth, *Nygmia phaeorrhaea*, Don., taken straight from hibernating nests, and again after feeding them for 3–4 days in a warm room. The results are presented in Table II.

TABLE II.

FREEZABLE WATER AND FAT IN CATERPILLARS OF THE BROWN-TAIL MOTH.

(After Sacharov, 1930.)

Temp. ° C.	% of water.	% of dry substance.	Ratio of frozen water to live weight.	Ratio of frozen water to total water.	Non-frozen water.	FAT. Ratio to live weight.	FAT. Ratio to dry weight.
			Caterpillars from hibernating nests.				
— 5·75	71·83	28·17	—	—	100	4·93	16·44
— 7·8	do.	do.	—	—	100	do.	do.
—11·1	do.	do.	3·63	5·06	94·94	do.	do.
—17·35	do.	do.	10·93	15·22	84·78	do.	do.
			Caterpillars fed for 3–4 days.				
— 3·9	82·94	17·06	—	—	100	2·52	12·46
— 5·75	do.	do.	4·13	4·98	95·02	do.	do.
— 7·8	do.	do.	37·20	44·85	55·15	do.	do.

This table (Table II) demonstrates clearly that feeding (or more probably, the activity due to higher temperature) resulted in an increase of total water content, while the quantity of fat decreased. The hibernating caterpillars withstood a temperature of — 17·35°, while as many as 82% of the active ones succumbed at — 7·8°.

For a comparison of a cold-hardy insect with a less resistant one, we may take Sacharov's data on the woodboring larvae of *Plagionotus arcuatus*, L., and the adult honey-bee, as shown in Table III.

The beetle larvae, containing only 54·12% of water, but 14·36% of fat, remained alive after exposure to a temperature of — 17·35°, honey-bees, with high water content (74·05%) and a small amount of fat (2·66%), began to die even at an exposure to the temperature of — 0·7°.

TABLE III.

Freezable Water and Fat in Larvae of *PLAGIONOTUS ARCUATUS*, L., and in Honey-bees. (After Sacharov, 1930.)

Temp. ° C.	% of water.	% of dry substance.	Ratio of frozen water to live weight.	Ratio of frozen water to total water.	Non-frozen water.	Fat Ratio to live weight.	[illegible] Ratio to dry weight.
			Plagionotus arcuatus, L.				
−11·1	54·12	45·88	—	—	100	—	—
−17·35	do.	do.	1·80	3·53	96·47	14·36	30·05
			Honey-bee.				
− 2·9	74·05	25·95	2·58	3·48	96·52	2·66	10·26
− 5·75	do.	do.	27·36	36·97	36·03	do.	do.
−11·1	do.	do.	54·72	73·92	26·08	do.	do.

These data by Sacharov, together with observations by Payne (*l.c.*) prove very convincingly that the degree of cold resistance in insects depends on the balance of easily freezable water and of fat in their bodies. The fatal point is, therefore, not constant in any insect species, but depends on the physiological state of the individual. The importance of this conclusion for the survival of hibernating insects is obvious (see p. 138).

The latest paper by Payne (1929) emphasises the importance of the absolute humidity of the air in the cold hardiness of insects. In the author's experiments the cold hardiness of the eggs of the moth *Hemerocampa leucostigma*, Sm., proved to bear a linear relationship to the absolute humidity. This relationship can be expressed by the equation :

$$T = K \cdot \frac{1}{H}$$

where T is the survival temperature in degrees centigrade, H, absolute humidity in millimetres of vapour pressure, and K, a constant.

A further important step towards the understanding of the problem was made by Robinson (1927, 1927*a*, 1928, 1928*c*, 1928*d*), who based his work on the relation between cold hardiness and the relative content of the free water and the water bound by the exceedingly minute colloidal particles occurring in enormous numbers in the protoplasm and in the intracellular liquids. These particles have a property under a falling temperature, of absorbing water, while under certain conditions they absorb also salts, or ions, from the solutions. The water taken up by colloidal particles is bound not within, but around them, so that it ceases to function as ordinary water, *e.g.* it will not freeze at — 20°. A comparative study of several insects unequally resistant to cold, proved that in the resistant species the amount of free water decreased considerably, and that of the bound water increased, on exposure to a low temperature. On the contrary, in non-hardy insects the relation between the free and the bound water changed very little on exposure to a low temperature. In an extremely non-hardy insect (*Sitophilus granarius*, L.) there occurred a rapid drop in bound water during the first few days at 0°. Connecting Robinson's investigations with those of Sacharov, it appears that fat may represent one of those hydrophilic colloids which regulate the balance between the bound water and the free water (freezable water in Sacharov's experiments). Again, dehydration which Payne applied for hardening insects, has an obvious effect on the balance between free and bound water.

Apparently, the process of binding water by colloids depends to a considerable extent on the time factor, since only this assumption would explain to some extent the hardening effect of gradual cooling. The influence of the velocity of cooling on supercooling and freezing points was observed by Bachmetjew, who studied the problem in detail (1901), but his conclusions are rather complicated and need not be discussed in detail here. It is sufficient to say that he found these points to vary sometimes in a direct correlation with the velocity of cooling, sometimes inversely. Verson (1871), working with the eggs of the silkworm moth, observed that they were able to withstand a temperature of — 32° if they were cooled to that point gradually, though rapid cooling was fatal. Observations of a similar kind can be found in other papers. They suggest that special attention should be directed to this point in future studies on cold resistance in insects.

The work by Payne, Robinson and Sacharov does not solve the problem of cold resistance in insects, but it shows the ways and methods for its solution. It is obvious that the problem is intimately connected with the most obscure phenomena of the bio-chemistry and bio-physics of metabolic water in living organisms, and it has to be attacked with corresponding methods instead of crude qualitative experiments.

(*c*) **Fatal Effect of Moderately Low Temperatures.**

The necessity of differentiating between the responses of an organism to the intensity and to the quantity of heat energy received from an outside source has already been pointed out (see p. 7). The same view holds good in the case of the action of low temperatures, since one insect may withstand freezing but be unable to survive a moderately low temperature acting for a long time, while another may be resistant to the quantity factor (prolonged moderate cooling), but non-resistant to freezing (Payne, 1927).

Some of the data presented in Table I (p. 9) suggest that the fatal effect of a low temperature depends on the length of exposure. Even not very low temperatures may cause death if acting for a long period. Exact investigations undertaken by Robinson (1926) on two species of grain weevils (*Sitophilus*) established the following periods of exposure necessary to kill at different temperatures (Table IV).

TABLE IV.

LOW TEMPERATURES FATAL TO *SITOPHILUS ORYZAE* AND *S. GRANARIUS*.

(After Robinson, 1926.)

Temperature.	Fatal exposure in hours.	
	S. oryzae, L.	*S. granarius*, L.
7·2°	160	875
— 1·1°	98	545
— 6·6°	14	100
—12·2°	3·5	70
—17·7°	1·5	2·5

These figures show clearly the specific differences in the cold resistance of two closely allied species, and the relation of mortality to the length of exposure.

Back and Pemberton (1916) found that no eggs or larvae of the Mediterranean fruit fly survived cold storage at 4·5–7·2° for seven weeks, at 0·5–4·5° for three weeks, or at 0–0·5° for two weeks.

Of particular interest are the experiments on bedbug eggs made by Hase (1930), who subjected the eggs to a moderately low temperature of 2° for varying periods of time and then incubated them at 25°. The data obtained by him are summarised in the following table (Table V).

TABLE V.

Influence of Moderately Low Temperature (2° C.) on the Eggs of the Bedbug. (After Hase, 1930.)

Days of exposure.	% of normal larvae.	% of larvae developed but not hatched.	% of undeveloped eggs.
10	80·0	3·3	16·6
15	66·6	10·0	23·3
20	36·6	20·0	43·3
25	26·0	10·0	64·0
29	12·5	10·4	77·1
35	5·5	2·8	91·6
39	0·0	—	100·0

It is significant that a long exposure to a low temperature results in a considerable percentage of eggs developing larvae which are, however, unable to hatch, and die in the egg. Even relatively short exposures to 2° are injurious, *e.g.* an exposure of three days resulted in the hatching of only 92·2% of eggs.

Data obtained by Carter (1925) in his work on *Bruchus obtectus*, Say, are similar to those obtained by Hase. He found that temperatures below zero, but not fatal in themselves, affect all stages of the insect: the pupae metamorphose only partially; adults may develop in the pupae, but fail to emerge; larvae may be unable to hatch from the eggs; etc.

Lengerken (1925) kept young larvae of *Tenebrio molitor*, L., first at the optimum temperature, then in a cool cellar. The length of larval life increased by many months and the larvae had many supernumerary moults. Most of the resulting pupae and adults were teratological and many adults were unable to copulate.

Frings (1901–1903) recorded a long series of observations on the fatal effect of moderately low temperatures on pupae of Lepidoptera, and further data on this subject can be found in papers by Bacot (1914, 1914*a*); Cornalia (1856); Back and Cotton (1924); Larson and Simmons (1924); Mell (1922); Merrifield (1890); De Ong (1921); Quajat (1883, 1903*a*).

The physiological side of the action of moderately low temperatures is not clear. From the data available it appears that death occurs only if the temperature is below the limit at which metabolism is reduced to a minimum. It is shown elsewhere (see p. 43) that different metabolic processes have different temperature limits, and it may be assumed, therefore, that at a certain low temperature some only of the normal metabolic processes are in progress, others being interrupted. This causes a disturbance of the physiological state of the organism, and if it goes on for a considerable period, death may result. These are, however, purely theoretical considerations and the problem awaits investigation by physiologists.

(*d*) **The Upper Fatal Limit.**

The following table (Table VI) of high fatal temperatures for different insects has been compiled to illustrate the general range of fatal temperatures. It should not be regarded as a summary of all the data available on the subject. (Supplementary data can be found in the papers by Alessandrini, 1907; Bachmetjew, 1901, 1907; Back and Cotton, 1924; Beattie, 1928; Bodenheimer, 1930; Bolle, 1878; Cantoni, 1872; Corte, 1923; Davenport, 1908; Gough, 1916; Janisch, 1928, 1930; Howard, 1924; Parker, 1924; Rudolfs, 1922; Storey, 1916; Yokohama, 1927; Zhmuidsinovitch, 1892; and in various monographs on injurious insects.)

TABLE VI.

Fatal High Temperatures.

Insect and stage.	Temperature.	Exposure in minutes.	Reference.
Coleoptera.			
Bruchus obtectus, Say, embryos	52	10	Back & Duckett, 1918.
do. do. newly hatched larvae	55	20	do.
do. do. full grown larvae	55	20	do.
do. do. pupae	55	25	do.
do. do. adults	55	4	do.
do. do. adults	50		Headlee, 1916.
Xylotrechus quadrupes, Chevr., adults	60	5	Boutan, 1907*a*.
do. do. do.	55	5–10	do.
do. do. do.	50	60	do.
do. do. do.	45–47	Some hours	do.
Anobium striatum, Ol.	42–46	0·5–1	Welch, 1924.
Lyctus brunneus, Steph.	45	1	do.
Sitophilus granarius & oryzae	48·8–55		Dendy & Elkington, 1920.
Rhizopertha dominica, F.	71		do.
Trogoderma granarium, Ev.	50–51	300	Husain & Bhasin, 1921.
Melolontha melolontha, L.	35–45	60	Faes & Staehelin, 1921.
Melanotus communis, Gyll.	45–49		Fulton, 1928.
Monochamus scutellatus, Say	43–50		Graham, 1924.
Ips pini, Say	44–50		do.
Chrysobothris dentipes, Germ.	45–52		do.
Carabus granulatus, L.	42·5		Koshevnikov, 1895–6.
Phyllopertha horticola, L.	42·5–43		do.
Neoclytus erythrocephalus, F.	40·5–57·2		Craighead & Loughsborough, 1921.
Lepidoptera.			
Butterflies, pupae	39–42		Frings, 1901–5.
Colias edusa, F., all stages	37–39		Hergula, 1927.
Porthetria monacha, eggs	56		Shemigonov, 1902.
Bombyx mori, eggs	53	5	Bellatti & Quajat, 1896.
Clysia ambiguella, Hb., *Polychrosis botrana*, Schiff., eggs	50–55		Chauvigné, 1920.
do. do. eggs & larvae	45	15	Dewitz, 1906.
Phalera bucephala, L., eggs & larvae	45	15	do.
Pyrausta nubilalis, Hb., larvae	58–74·5	11–6	Worthley & Caffrey, 1927.
Platyedra gossypiella, Saund., larvae	Over 52	5	Storey, 1917.
do. do. do.	54·5	60	Ohlendorf, 1926.
do. do. do.	102·5	5	do.
Ephestia kuehniella, Z., eggs	34·4		Hase, 1927.

TABLE VI.—*Continued.*

Insect and stage.	Temperature.	Exposure in minutes.	Reference.
Hymenoptera.			
Apis mellifera, L., drones . .	Over 55	2–0·6	Kozhevnikov, 1895–6.
do. do. workers . .	44–57	do.	do.
Vespa	47·5	do.	do.
Hemiptera.			
Oxycarenus hyalinipennis, Costa, eggs	48	240	Kirkpatrick, 1923.
Toxoptera graminum, Rond., wingless adults	37		Glenn, 1909.
Phylloxera vastatrix, L., hibernating adults	Over 45		Cornu, 1878.
Diaspine Coccids . . .	54–55		Reh, 1900.
Orthoptera.			
Acridid larvae	60–90	0·5–2	Antonov, 1922.
Locusta migratoria, L., hoppers .	31·5–48	5	Nikolsky, 1925.
Melanoplus mexicanus, Sauss., & *Camnula pellucida*, Scudd., eggs	60	20	Parker, 1930.
do. do. larvae	54	10	do.
do. do. adults	58	10	do.
Blatta orientalis, L. . . .	41		Graber, 1887.
do. do. . . .	33		Bütschli, 1874.
Diptera.			
Glossina morsitans, Westw., puparia	47·77	30	Chorley, 1929.
Culex pipiens, L., adults . .	44·4–45		Rudolfs, 1925.
Aphaniptera.			
Fleas	30·5–31·5	45	Cunningham, 1911.
Anoplura.			
Pediculus vestimenti, L. . .	50–55	15–25	Engelhardt, 1915.
Protura.			
Podura similota	35		Nicolet, 1841.

A study of this table (Table VI) shows that the upper fatal limit is fairly uniform for various insects, and lies on the average at about 50°. The available data are not all comparable, since many authors paid no attention to the fatal time of exposure to a given temperature, while it is clear from some observations that this is a very important factor. For example, in the case of the beetle *Xylotrechus quadrupes*, Chevr., it is necessary to expose the insect to a temperature of 45–47° for several hours, to produce death, while five minutes are sufficient to kill it at 60° (Boutan, 1907*a*).

Several authors have pointed out that there may be considerable individual variation in the resistance to high temperatures of individuals of the same species. Gauckler (1886, 1897) subjected twelve pupae of *Celerio euphorbiae* to a temperature of 87°, with the result that eleven of them were killed, but one survived and produced a healthy adult. Graham (1924) studied the individual variation in the fatal high temperature on *Monochamus scutellatus* and found it to vary from 43° to 50° in the case of the adults and from 45° to 50° in the larvae.

Such individual variations in the resistance may be of considerable importance for the survival of the species during abnormally high temperatures.

The combined action of temperature and humidity is an important factor amongst those affecting the resistance to heat. This combined action is discussed later (see p. 81). Bachmetjew (1907) drew attention to the importance of the water-content of the insect body in this connection and suggested that insects containing more water would die at a given high temperature more quickly than those with less water. This problem has, however, apparently not been studied, but it would be of considerable interest, since during droughts insects are subjected to a greater evaporation and obtain less water with their food than in normal conditions; at the same time it is during such periods that they are exposed to abnormally high temperatures.

It is not proposed to discuss here the physiological reasons for the fatal action of high temperatures on the insect organism. It is sufficient to observe that there exists a great difference between the action of cold and of heat; both produce stupor at first, but while an insect, which is so frozen as to become hard, may be revived by raising the temperature, the stupor produced by heat is invariably fatal, provided the exposure is sufficiently long. Thus, the action of heat is irreversible (Matisse, 1919).

An exposure to a high temperature may very often have no apparent immediate effect on the vitality of an insect, but the subsequent development and the length of life are often very seriously affected even by short exposures. This fact is of a great biological importance, but it will be more convenient to discuss the data on this subject in connection with other factors affecting the longevity of insects (see p. 50).

(*e*) **Development at Constant Temperatures.**

Before discussing the influence of heat on the development of insects, we must define clearly what exactly is meant by development. The necessity of defining such an obvious term arises out of the recent proposal by Janisch (1930) to regard as the full period of development of an organism the amount of time which has to pass from the beginning of the embryonic development to the physiological death resulting from old age. Viewed from this point the development of an insect comprises a number of entirely different processes, such as the formation of the embryo, the growth of the larva, the histolysis of larval tissues and organs, the formation of imaginal organs in the pupa, the sexual development of the adult, and the process of senescence. The last process can scarcely be included in the general development of the organism, and most biologists regard senile decay not as a direct continuation of development, but rather as an opposite process. Thus, by development is usually meant the processes of building up an organism, beginning with the embryonic development and ending with sexual maturity. Even with this limitation it appears both unscientific and impracticable to study the general rate of development throughout all its stages, since the partial processes of development are affected by external factors in a different way. Each partial process of development and the effects of external factors on it must be studied separately. This course has been and is being followed by practically all investigators. Of course the full duration of life (not of development) under different conditions can also be studied, but this is an entirely different problem, which is discussed separately (see p. 50).

(i) *Temperature range of development.*

The fact that at a certain low temperature all insects become inactive points to an interruption of metabolic processes. It follows that the processes of development are possible only at the temperatures above a certain point. This theoretical point has received several names from different authors, and the most inappropriate of these is the "critical point," since this name has been applied to mean the lower fatal temperature, the point at which development starts. "Physiological zero" is another name commonly and somewhat vaguely used, but it would be better to restrict this term to the lower temperature point, below which no metabolic processes can occur. That the physiological zero coincides with very low temperatures has been demonstrated by several authors, who have worked on the basal metabolism and respiration of insects at low temperatures (see p. 43).

"Minimum effective temperature" is a suitable term for the point under discussion, but the name "*threshold of development*" expresses the idea still more clearly. The threshold of development can be defined as the temperature at which, on the descending scale, the development definitely ceases, and at which, on the ascending scale, the development is initiated (Peairs, 1927). According to this definition an insect can be kept at this temperature without any changes for an indefinite period (Sanderson and Peairs, 1913). This is, of course, only a theoretical possibility, since we know that long exposures even to moderately low temperatures may be fatal (see p. 15).

The practical difficulty of determining the exact threshold of development for a given stage of an insect is evidently very great, since it is scarcely possible to register by any method a very small amount of development going on at a very slow rate. Most authors have evaded this difficulty by accepting as the theoretical threshold the point at which the reciprocal curve of development intersects the temperature axis (see p. 25), but Peairs (1927) and Shelford (1929) have shown that this is only approximately correct (see p. 29).

Another method of calculating approximately the threshold of development has been offered by the phenologist Oettingen (1879) and adopted by Shelford (1927, 1929). A series of observations is made on the length of the development period at different constant temperatures. Then several probable values for the threshold are assumed, and the temperatures above the threshold are multiplied by the time. That value which gives the most nearly constant product within the widest range of temperature may be chosen as correct.

Actual determination of the threshold could be made only by observing the development of an insect stage at several low temperatures, and it was in this way that most of the known threshold values were obtained. An old conception that a temperature of 6·1° (43° F.) is the starting point for development generally has proved to be incorrect, since not only different insects, but different stages of the same insect have different thresholds. Thus, Sanderson (1910) found that the threshold for the grain aphis, *Toxoptera graminum*, Rond., is 1·65°, while for the egg and larva of the codling moth it is about 10°, and for the pupa 11·1° (Glenn, 1922*a*). 11° has also been stated by Hergula (1927) to be the threshold of development of all stages of *Colias edusa*, F. Blunck (1923) determined the thresholds of development for all stages of *Dytiscus marginalis*, L.; that for the eggs was about 0°, for the larva of the first stage 1°, for the second stage 3°, and for older stages 3·8°. According to Shelford (1927) the threshold is not a fixed point, but varies, within certain limits, with the humidity and other factors, as well as with the generation and the individual. For the larvae of the codling moth it varies from 6·1° to 8·8° for the pupa; for the eggs from 6·7° to 9·4°, and for the hibernated larva from 6·1° to 10°. Acqua (1922; 1929) recorded that the embryonic development of the univoltine race of silkworms begins at 12°, but in the bivoltine race a temperature of 6° is sufficient for this purpose. Fischer (1896) and M. Townsend (1926) observed that the development of lepidopterous pupae does not stop entirely at 0°, and Hase (1930) even expressed the opinion that a developmental zero is physiologically non-existant, since certain metabolic processes can occur even at temperatures near the zero point of the thermometer. This opinion, however, is clearly due to not differentiating between the physiological zero and the threshold of development. That the latter is not a fiction is sufficiently proved by the interruptions in the development caused by low temperatures during winter (see p. 104).

An attempt to check histologically the deterrent influence of low temperatures on the development has been made by Schuckmann (1909). This author studied various organs of normal butterfly pupae and of those subjected to a temperature of — 8°, and found that the low temperature actually brought to a standstill all processes of metabolism and metamorphosis. The temperature studied was, however, clearly below the threshold of development, and it would be of interest to apply the same method to the study of the development at a range of temperatures around the possible threshold.

Nothing appears to be known as to the physiological factors responsible for the threshold of development, *i.e.* exactly what are the processes inhibited by a low temperature. In one case the threshold is known to be connected with the conditions of nutrition. I refer to the work by Werner (1926) on the larva of *Potosia cuprea*, F., which feeds on cellulose, digesting it with the help of bacteria, and which does not grow at temperatures below 10°, this being the minimum temperature for the fermentation of cellulose.

Still more unsatisfactory is our present knowledge of the *upper temperature limit of development.* Indeed, it is doubtful whether this point is distinct from the upper fatal limit.

A high temperature sufficiently near the point at which the development is interrupted almost certainly causes certain irreversible physiological disturbances. If there existed an appreciable interval between the upper limit of development and the upper fatal point, we should be able to observe a quiescent state of a developing insect at that range, similar to the quiescence at the temperatures below the threshold of development and above the lower fatal point. But no such phenomenon is known. (Aestivation, *i.e.* quiescence at relatively high temperatures, is due to the unfavourable humidity conditions, not to those of heat; see p. 108.)

Not all temperatures within the effective range are equally favourable to development, since on one hand, the velocity of development, generally speaking, increases with the rise in temperature, decreasing again near the upper limit, and on the other hand, the percentage of individuals accomplishing development successfully also depends on the temperature. When considering the *optimum range* we may take as such the range at which the rate of development is the highest, but this occurs near the upper limit, and is accompanied by a high percentage of mortality. It is, therefore, more correct to accept Blunck's (1914) and Peairs' (1927) definition of the optimum as a temperature range at which the relatively greatest percentage of individuals accomplish their development within the relatively shortest period. The optimum defined in this way becomes of great theoretical and practical importance, comprising both the rate of development and the percentage of survival. Unfortunately, very few authors have paid attention to both factors, so that we know very little about the optimum, though it should be determined for each stage of all the more important pests. In the case of the eggs of *Dytiscus marginalis*, L., the optimum range is 10–15°, while the threshold of development is 0°, and the upper limit about 30°

(Blunck, 1914). Of course, it is natural to expect that the optimum range for a given stage is not absolutely constant, but is subject to some variation, which depends on other factors (humidity, etc.), and on the individual. This consideration does not affect the practical importance of the optimum, for which the average value can and must be found.

(ii) *Rate of development.*

The earliest experiments on the relation of the velocity of development of insects to heat were made by Bonnet (1779), who studied the rate of reproduction of *Aphis evonymi*, F. The data obtained indicated that the period necessary for the development of a parthenogenetic Aphid from birth to maturity was in inverse ratio to the average temperature during the period. Numerous observations of the same character have been made by other authors, but it would not serve any useful purpose to review their work, which, although including some exact figures, did not go beyond the stage of the accumulation of facts. (Bachmetjew, 1907, presented a review of the literature previous to his work.)

(iii) *Thermal constant.*

The first theory put forward with regard to the relation between temperature and the rate of development of insects was taken from botanists. This was the theory of the *thermal constant*, according to which the completion of a given stage in development requires an accumulation of a definite amount of heat energy. The theoretical truth of this assumption can scarcely be disputed, but in practice it has proved to be impossible to measure actually the amount of heat energy, which should be represented in calories. A method of summing up temperatures acting during a day, or day-degrees, was therefore adopted. Since it was obviously incorrect to sum up all temperatures, including those not sufficiently high for development, only the temperatures above the threshold of development, *i.e.* the effective temperatures, were taken into consideration. Older authors assumed somewhat arbitrarily, and incorrectly, that the threshold of development for various organisms is approximately the same, viz. 43° F. or 6·1° C. Later, a number of investigators (particularly Sanderson, 1910; Sanderson and Peairs, 1913; Peairs, 1914, 1927; Blunck, 1914, 1923; Glenn, 1922, 1922*b*; Martini, 1925; Lathrop, 1923; Kiseleva, 1928; Bodenheimer, 1926; and others) applied an improved method of summing up temperatures, basing their calculations on the actual threshold of development for the particular insect and stage.

Extensive experimental work on breeding various insects at different constant temperatures carried out by Sanderson, Peairs and Blunck (*ll.cc.*), enabled them to find a mathematical expression for the correlation between the period of development and heat. When plotting the periods of development and the respective temperatures, they obtained curves which, on examination, proved to be true equilateral hyperbolae with the formula

$$(T - K)D = C$$

where T is the temperature during the experiment, K is the threshold of development, D is the duration of the stage at that temperature, and C is the thermal constant. This formula means that the product of the effective temperature and the time is always a constant. This can also be seen from the curve (Fig. 2), since in a hyperbola the abscissa of any point on it multiplied by the ordinate produces a constant value. The abscissa in this case is the length of development, and the ordinate is the temperature.

From the same formula it will be seen that the length of development is inversely proportional to the temperature, viz. :—

$$D = \frac{C}{T - K}$$

When two points of a curve have been determined experimentally, these formulae enable one to calculate its other points and to plot the whole curve. They make it possible also to calculate the threshold of development from the data of two experiments at different temperatures, using the following two equations :

$$(T - K)D = C$$

$$(t - k)d = c$$

and consequently :

$$K = \frac{dt - DT}{d - D}$$

The correctness of the formula is proved by the fact that the calculated values of the heat required to complete development within a definite number of days are in close agreement with the empirical values, as is shown by the following table by Blunck (Table VII).

TABLE VII.

Development of the First Larva of *Dytiscus marginalis*, L., at Different Temperatures. (After Blunck.)

Length of development (days).	Required temperature, ° C.	
	Calculated.	Empirical.
4	21·8	Over 20
5	19·5	18·6–19 and over
6	18·0	18–19·2
7	16·9	17–17·6
8	16·1	16·8–17·4
9	15·4	14·1–15·7
10	14·9	13·8–14·4
11	14·5	13·9
12	14·2	13·5–14·4
18	12·9	12–13
26	12·1	12
39	11·5	11–12

It is known that the reciprocal of a hyperbola is a straight line, and this fact helps still further to simplify the calculations. In the foregoing hyperbola the days were plotted as abscissae and the temperatures as ordinates. To obtain a reciprocal it is necessary to plot temperatures as abscissae, while the reciprocal values of the length of development serve as ordinates. Such reciprocal values are obtained by dividing a unity (*i.e.* the whole development) by the number of days (or hours) it takes, and they represent the fraction of the whole development which takes place in a day (or an hour). This fraction is called the *develop-*

mental unit (Prochnow, 1907, 1908, 1914; Sanderson, 1910; Shelford, 1926, 1928, 1929. Janisch, 1930, introduced the same conception as an entirely new

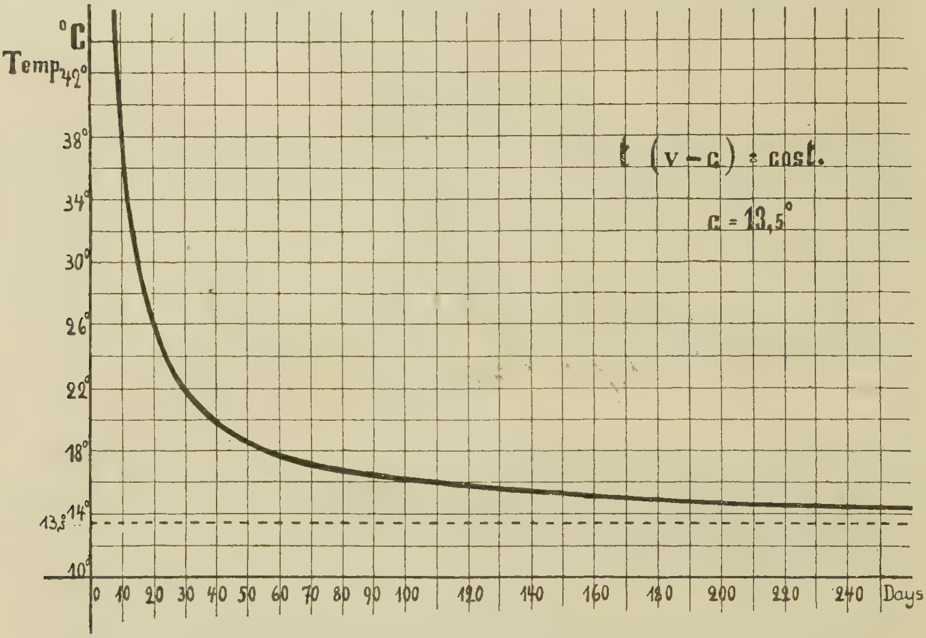

FIG. 2.—The hyperbola expressing the length of the development of *Ceratitis capitata* at different temperatures according to the thermal constant theory. (After Bodenheimer, 1926.)

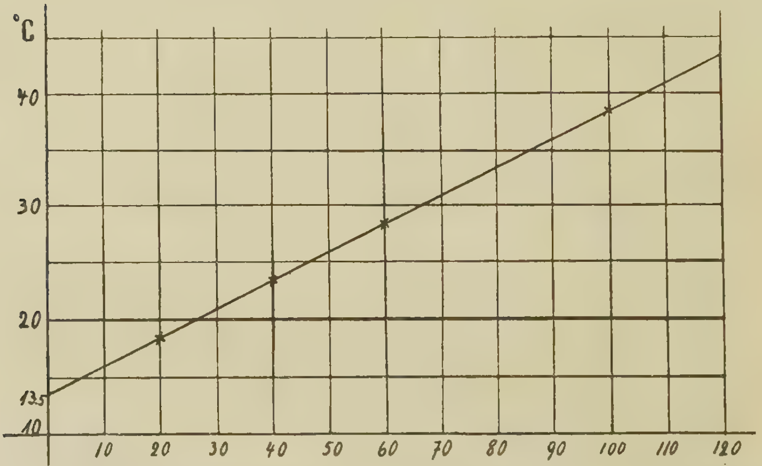

FIG. 3.—The straight line, reciprocal of the hyperbola of Fig. 2, expressing the development index of *Ceratitis capitata* at different temperatures. (After Bodenheimer, 1926.)

one). In other words, the reciprocal value expresses the relative velocity of the development, and the line based on these values shows the rate of acceleration of development with the rising temperature (Fig. 3). This line is called the *velocity line* or the *index line,* and any point on it is the *development index* for the given temperature. The point where the index line crosses the temperature axis is the theoretical threshold of development, or the K value of the above formulae.

To illustrate the actual procedure of the calculation and the construction of the hyperbola and of the index line, the following example may be taken (Bodenheimer, 1928).

The empirical data show that the total development of the Mediterranean fruit fly takes 20 days at 26·0°, and 41·7 days at 19·5°; and that the threshold of development calculated by the formula given above is approximately 13·5°. The thermal constant would be, therefore, 250. These data make it possible to calculate the co-ordinates for any point of the index line, as is shown in Table VIII.

TABLE VIII.

CALCULATION OF DEVELOPMENT INDICES OF *CERATITIS CAPITATA.*
(After Bodenheimer.)

Temperature.		Length of development in days.	Development index.
Observed.	Effective.		
43·5	30	8·3	0·120
38·5	25	10	0·100
33·5	20	12·5	0·080
28·5	15	16·6	0·060
23·5	10	25	0·040
18·5	5	50	0·020
16·5	3	83·3	0·012

From this table (Table VIII) the straight line of Fig. 3 can be easily constructed, and this represents the index line for the development of the fly at different constant temperatures. Bodenheimer (1928) collated sufficient data from the literature to construct the hyperbolae and index lines for twenty-five different species of insects of economic importance. Sanderson and Peairs (1913) and Peairs (1927) published the results of special breeding experiments arranged in order to obtain the necessary data and the resulting curves and reciprocals. The paper by Peairs is particularly important, since the work was arranged mainly in order to test the straight line character of the temperature-velocity relation. The deviations of the experimentally determined points from the straight line, within the medial range of temperatures, proved to be very slight and usually within the limits of observational error. This means that the straight line, and consequently the hyperbola, represents the temperature influence on the duration and rate of development with a sufficient exactitude. It may be mentioned that Friend (1927) found that the velocity line is not straight but sigmoid. Shelford (1929), however, considered his data inadequate for forming a definite conclusion. Supplementary data on the thermal constant theory can be found in the papers by Bodine, 1925; Chapman, 1927; Glenn, 1922, 1922*b*; Headlee, 1928; Heller, 1928, 1930; Kiseleva, 1928; Knoche, 1908; Krogh, 1914*b*, 1914*d*; Lathrop, 1923; Loeb and Northrop, 1917. Strachov-Kolchin, 1915, and Lebedev, 1924, obtained quite independently a curve similar to a hyperbola.

For the sake of completeness it may be mentioned that several authors have attacked the thermal constant theory on the ground that it does not hold good if actual temperatures are used (Hennings, 1907, 1907*a*; Hunter and Hinds, 1904; Bodenheimer, 1928; Uvarov, 1929). Indeed the figures, *e.g.* those for the development of *Ceratitis capitata* quoted in Table VIII show that the "sum of temperatures," if actual temperatures are taken into consideration, varies from 361·1° to 1374·5°. This, however, is not the case if only effective temperatures, *i.e.* those above the threshold of development are considered. The criticism of these authors is, therefore, based on a misunderstanding.

Much more serious are the objections to the straight line temperature-velocity relation raised by several investigators as a result of observations on the development at temperatures near the possible limits.

Prochnow (1907, 1908) was undoubtedly the first to discuss the velocity curve in its whole course. His experiments on the development of the eggs and pupae of various insects were not conducted at constant temperatures. The insects were kept for a part of the time at a medial temperature, were then transferred to a high or a low one, after which the development was permitted to proceed until the end of the stage at the medial temperature. For calculating the velocities, the following method was used. The whole development, which is a constant quantity for the given stage of the species, was designated as a unity. The part of development accomplished at the temperature t, was called X_t, so that the whole stage would have been accomplished at this temperature in $\frac{1}{X_t}$ hours. The experimental data on the actual length of exposure to each temperature enabled the construction of a series of equations, such as the following:

$$\begin{aligned} 8X_{22\cdot 0} + 192X_{11\cdot 5} + 126X_{19\cdot 7} &= 1 \\ 8X_{22\cdot 0} + 196X_{16\cdot 5} + 35X_{20\cdot 7} &= 1 \\ 8X_{22\cdot 0} + 136X_{21\cdot 5} &= 1 \\ 8X_{22\cdot 0} + 45X_{24\cdot 9} + 67X_{21\cdot 8} &= 1, \text{ etc.} \end{aligned}$$

The X values for the limits 19–22° are obtained by graphic interpolation, or extrapolation, by means of which all other equations can be solved. Since the velocity values are only relative, it is convenient to multiply them by 10,000. Table IX shows the relative velocity of development at various temperatures.

On the basis of this table (Table IX) Prochnow drew curves for each species and constructed an average curve of velocities as dependent on temperatures. This curve has been re-drawn in Fig. 4, since the original curve was drawn with the temperatures as ordinates and the velocities as abscissae. The curve presents the following features: the velocity of development above the lower limit increases at first slowly up to about 15°; then the acceleration becomes more rapid, but close to the peak of the curve a falling off of the velocity becomes evident. Beyond the point of the maximum velocity the curve descends very steeply. A less rapid decrease near the upper limit is shown in the curve, but on purely theoretical grounds. No mathematical formula has been developed by Prochnow to express his curve.

Prochnow's work apparently remained unknown to Krogh (1914*b*, 1914*d*), Peairs (1914, 1927), Loeb and Northrop (1917) and Shelford (1926*a*, 1928, 1929), who also reached the conclusion that the process of development at extreme temperatures cannot be expressed by the continuation of the straight line of velocities, but that the curve deviates near both ends in opposite directions (Fig. 5).

TABLE IX.

Relative Velocity of Development of some Insects at Different Constant Temperatures. (After Prochnow, 1908.)

	Temperature, ° C.								
	11·3–12.	14·6–16·5.	19·9–22·0.	24·0–25·2.	28·0–30·2.	30·9–33·1.	35·7–36·3.	39·0.	40·0.
Microgaster nemorum, Htg., pupa . .	19	27	65	71	65	—	—		
Teleas sp., pupa . .	7	8	25	35	44	43	—		
Sphinx pinastri, L., eggs	12	30	58	82	87	80	67		
Dendrolimus pini, L., eggs . . .	4	19	36	46	54	46	31		
Nygmia phaeorrhoea, L., eggs . . .	13	20	43	68	74	70	—		
Acronycta menyanthidis, View., eggs . .	15	37	69	99	130	139	115		
Naenia typica, L., eggs.	10	35	63	74	88	73	—		
Vanessa io, L., pupa .	9	19	29	56	61	63	24		
Vanessa urticae, L., pupa . . .	6	16	37	58	77	77	70	25	6
Vanessa polychloros, L., pupa . . .	11	13	25	47	56	68	40		
Vanessa antiopa, L., pupa . . .	8	13	28	40	55	56	37		
Nygmia phaeorrhoea, L., pupa . . .	3	8	20	27	36	39	—		
Leucoma salicis, L., pupa . . .	8	20	37	59	65	66	—		
Porthetria dispar, L., pupa . . .	9	17	25	37	52	46	—		
Catocala nupta, L., pupa	—	7	18	24	29	30	17		

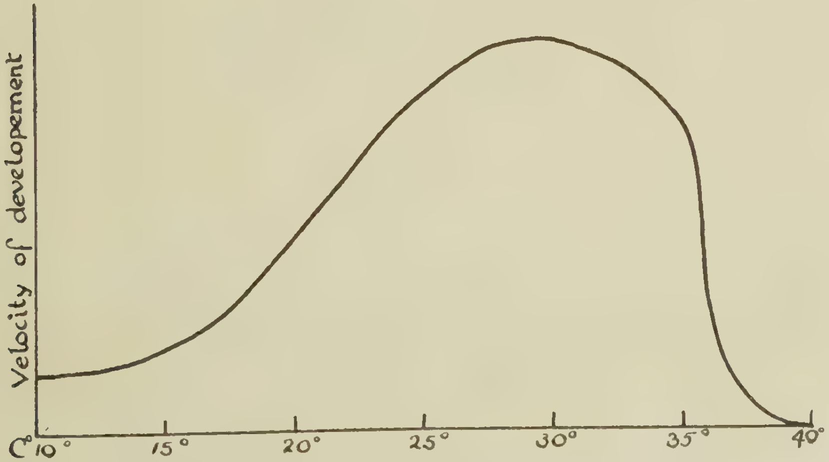

Fig. 4.—Prochnow's curve of the velocity of development in relation to the temperature. (Re-drawn after Prochnow, 1908.)

The similarity of Prochnow's and Shelford's curves is very significant, since they obtained them quite independently and by different methods.

On the basis of experimental evidence of this kind, Shelford, in several recent papers, has offered a most vigorous criticism of the thermal constant theory. To use his own expression "the idea, now centuries old, to the effect that temperature can be summed so as to give approximately the time of development of a particular organism must be abandoned wherever accurate results are desired." He insists, therefore, on the summing up of developmental units, instead of temperatures, and this is undoubtedly a more correct method. At the same time, however, the curves given by Shelford (see Fig. 5) coincide, within a certain medial range of temperatures, with the temperature-velocity straight line, and it makes no difference whether the temperatures or the developmental units are summed up within that range, both being numerically equivalent. Thus, there is only more or less a formal difference between summing up the temperatures and the developmental units, unless the experiments are made at extreme, or at fluctuating, temperatures, when the summing up of developmental units gives more correct results than that of the temperatures. In other words, the summing up of developmental units is a more exact method, applicable to all temperatures, while the use of a thermal constant is restricted to the medial range of constant temperatures. With this limitation the latter method is perfectly sound and Shelford's criticism of it appears unnecessarily severe.

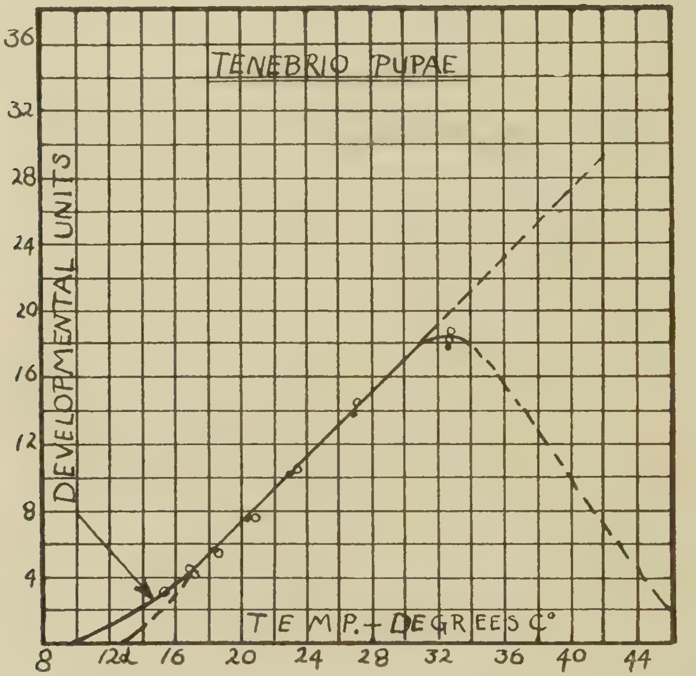

FIG. 5.—The curve of the development of *Tenebrio* pupae based on the development unit theory. (Re-drawn after Shelford, 1929.)

The observations on the deviation of the velocity curve near its lower end from the straight line have an important bearing on the position of the threshold of development. The straight-line theory assumed, as we know, that the threshold coincides with the point at which the straight line intersects the temperature axis. This, however, now proves to be not always true. Shelford has suggested that the crossing point should be designated *alpha*, thus stressing its purely mathematical significance, and insisting that it has no relation to the actual threshold of development, for which it has been taken by other authors. That this objection is again mainly formal can be seen from the fact that Shelford himself (1927) recommends a graphic method for finding the *alpha* value. The method consists of drawing a straight line through the empirically found velocities for different temperatures. Such a line will cross the temperature axis at approximately the *alpha* value, and, if averages for the points within one degree of each other are used, the results of the method are recognised by Shelford as satisfactory. In other words, the deviation of the velocity curve, indicating a relative acceleration of the development as compared with the straight line, is not important. This, of course, does not affect the great theoretical value of the deviation, as well as its practical importance. These aspects have been analysed rather fully by Janisch and they will be discussed later.

As regards the deviation near the upper end of the velocity line, Glenn (1922, 1922*a*, 1922*b*) was one of the first to pay attention to it in connection with forecasting the dates of appearance of the stages of the codling moth.

(iv) *van't Hoff's rule.*

The rule of van't Hoff was developed originally with reference to chemical reactions. It states that the velocity of a reaction increases with the temperature, and the coefficient (Q_{10}) expressing the rate of the increase has a value of between 2 and 3 for each ten degree interval. A considerable number of attempts have been made by biologists to apply the rule to the relationship between the temperature and the velocity of development. The calculation of Q_{10} showed, however, that only in relatively few cases, and within a limited range of temperatures, did the coefficient approach the value of from 2 to 3 as required by the rule, and that it may vary from one to a very high value, since the Q_{10} value normally does not remain constant at different temperatures, but varies. The curve expressing the relation would be an exponential one, its reciprocal being not straight, as in the case of a hyperbola, but sigmoid (see Fig. 6, H). The formula of the curve is

$$Q_{10} = \frac{D_2}{D_1}\left(\frac{10}{t_1 - t_2}\right)$$

where t_1 and t_2 are two different temperatures, D_1 and D_2, the length of development at the two temperatures.

The following modification of van't Hoff's formula was offered by Arrhenius :

$$D_2 = D_1 e \frac{q}{2} \cdot \frac{t_2 - t_1}{t_2 \cdot t_1}$$

where q is the so-called, critical thermal increment or coefficient. This coefficient proves to be inconstant in the case of development, although it is of some importance in other metabolic processes.

Without entering into a detailed criticism of van't Hoff's and Arrhenius' rules, it may be stated that neither is of much value in the study of the interrelations of development and heat. The fact that some authors have succeeded in fitting their results rather closely to the requirements of these rules only proves that the actual curves expressing them differ but little from each other. Indeed, Martini (1928) pointed out rightly that quite a number of different curves can be made to agree with the experimental data so long as extreme cases are not considered.

(v) *Exponential curve of Janisch, and other curves.*

If we compare the hyperbola of the thermal constant theory and van't Hoff's exponential curve (Fig. 6, T and H), we see that within certain limits they have a similar course. Janisch in his experiments on the Flour moth (1925–1928) suggested that the results agree best with a catenary exponential curve (Fig. 6, E), which again does not differ much from the other two curves within the medial temperature limits. The reciprocals of the three curves (Fig. 6, dotted lines), however, differ considerably. The reciprocal of the hyperbola, *i.e.* the straight line, disagrees with the experimental data near both ends. The reciprocal of the van't Hoff's curve is sigmoid and does not fit the empirical data, especially at the upper end where it deviates in such a way as to suggest a relative acceleration of the velocity at high temperatures, while exactly the opposite, in fact, takes place. The reciprocal of the catenary curve presents deviations at both ends, and is, thus, more in agreement with the experimental data. Almost exactly the same type of reciprocal curve of velocities has been found empirically by Prochnow (see p. 26 and Fig. 4), whose work has been overlooked by Janisch.

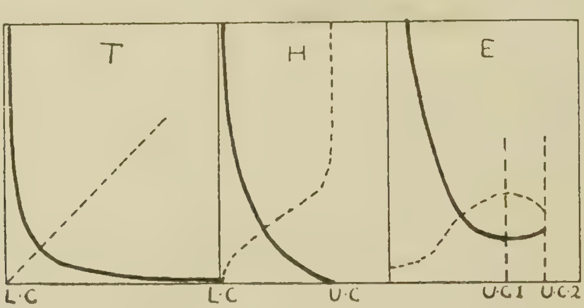

Fig. 6.—Curves of the length of development (black line), and their reciprocals expressing the velocity of development (dotted line). T, the hyperbola of the thermal constant theory; H, the curve of van't Hoff's rule; E, the exponential curve of Janisch; L.C., lower critical point; U.C., upper critical point. (Re-drawn after Janisch, 1928.)

Janisch distinguishes two upper critical points, one (U.C.1 of Fig. 6, E) being the point above which the organism can live but is unable to complete its development, and the other (U.C.2) which is the fatal point. He extended his ideas to cover a whole series of biological phenomena as affected by heat. The " exponential law " appeared to him a universal biological law, and in his book published in 1928 he collected a considerable amount of data, mainly non-entomological, to support his views.

His theory, however, met with a very serious criticism on the part of Martini (1928). This author points out that Janisch's curve does not fit the experimental data any better than a hyperbola. A positive feature of the exponential catenary curve is that it draws special attention to the behaviour of the organism at extreme temperatures. This, however, has been done by several other authors (see above). On the whole, Martini is of the opinion that the work of Janisch is far too theoretical to be of direct use for the understanding of the relationship between heat and development and that his curves have no special advantage over the hyperbola of the thermal constant theory, which is much simpler to use. This criticism has been answered by Janisch in his latest paper on *Prodenia litura*, F. (1930), in which, however, he presents mainly mathematical arguments in support of the catenary curve as against the hyperbola, while his experimental data are anything but numerous and, moreover, do not extend to the important lower end of the curve. It must be mentioned also that Janisch's conception of development differs from that of all other authors (see p. 19).

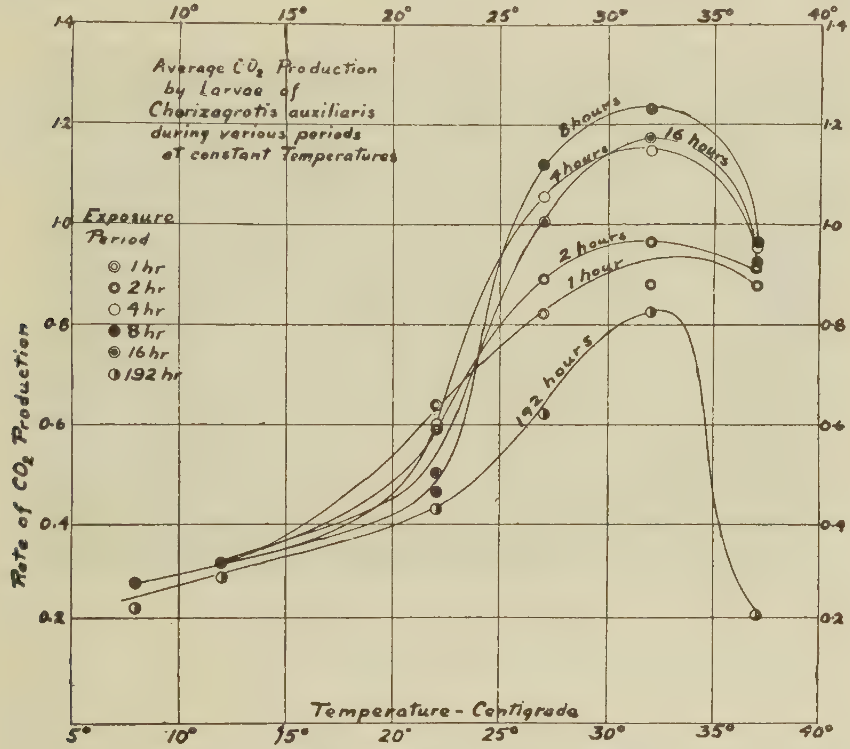

Fig. 7.—Average carbon dioxide production by cutworms during various periods at constant temperatures. (After Cook, 1927.)

Cook (1927) working with cutworms obtained curves which are also of the exponential catenary character. These were asymmetrical, as shown in Fig. 7, which represents the CO_2 production by the larvae at different constant temperatures. The curves for the velocity of development were of the same type. This curve of velocities is almost identical with Prochnow's empirical curve (see p. 27), *i.e.* it rises rather slowly at first, then rapidly approaches a maximum, where it slows down to a standstill, and then rapidly drops to zero. The curve may be explained as a balance between an increasing rate of activity on the part of an enzyme stimulating the metabolism, and a similarly increasing rate of destruction of the enzyme at high temperatures, which results in the total destruction of the enzyme within a short period. Substantially the same idea has been expressed by Duclaux (1899).

It appears probable that the curves of velocity suggested by Cook will fit the experimental data on the development of various insects, but so far they have not been subjected to sufficiently extensive tests, so that it is difficult to judge to what extent the asymmetrical catenary curve can be used in connection with temperature experiments.

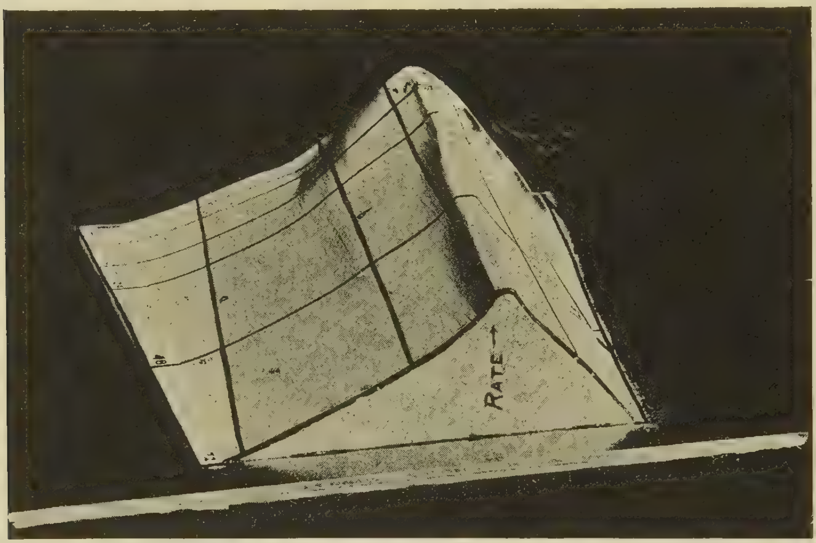

Fig. 8.—Solid three-dimensional model representing the relation of time and temperature to growth. The time scale is along the left-hand margin, the temperature along the front margin, the rate of growth on the vertical axis. (After Cook, 1927.)

The latest idea with regard to the curves of the velocity of development is to represent the relation by a three-dimensional curve. The use of three dimensions is necessary since there are two variable factors involved, viz. the temperature and the length of exposure. This type of curve was first proposed by Matisse (1919) for expressing the influence of temperature on locomotion. Cook (1927) constructed a model of a three-dimensional curve for metabolism (Fig. 8). The time scale is shown along the left-hand margin, the temperature scale along the front edge, and the rate of development is represented by the vertical axis. The idea of a three-dimensional curve is scientifically sound, but its practical application is scarcely possible.

(vi) *Variation in the rate of development.*

Most of the papers quoted above were concerned with the average rate of development, but it should be realised that differences in the rate between individuals of the same species, kept under identical conditions, may be very considerable. The complete development period of the codling moth was found by Glenn (1922) to be very variable, the total effective day-degrees varying from 814 to 1475. A certain portion of this range of variation is due to inaccurate observations, but there can be no doubt that purely individual factors are also involved. This necessitates the use of averages in all calculations and renders the latter always approximate only, so that polemics as to the exact shape of curves, etc., appear to be somewhat futile.

Apart from purely individual variations, there is variation in the rate of development under similar conditions between individuals belonging to different generations (Shelford, 1927). Again, Bonnier (1926) found a regular difference in the number of hours required for the development of the two sexes of *Drosophila* as follows (Table X).

TABLE X.

THE TIME OF DEVELOPMENT OF *DROSOPHILA* AT DIFFERENT TEMPERATURES.
(After Bonnier.)

	25°.		30°.	
	Larva.	Pupa.	Larva.	Pupa.
	hours.	hours.	hours.	hours.
Males	116·78	115·46	103·37	84·26
Females	116·62	111·36	99·95	78·15

Bliss (1926) also recorded that the rate of development of females of *Drosophila* is 1·03 of that of the males, the ratio being greater at higher temperatures. Przibram (1909) observed that the rate of growth of the larvae of *Mantis religiosa*, L., was rather higher in the females than in the males.

There is scarcely any need to point out that the rate of development and the optimum temperature may, and do, vary to a considerable extent in different stages of the same insect (Fielde, 1905; Ludwig, 1928; Sikora, 1915; etc.).

Further data on the influence of temperature on the rate of development can be found in the papers by Acqua, 1929; Ballard and Evans, 1928; Bonnet, 1779; Bonnier, 1926; Chapman, 1928; Dean, 1924; Ewing, 1916; Fielde, 1905; Giusti, 1903; Hase, 1927; Hein, 1923; Hunter and Hinds, 1904; Kanitz, 1915; I. Klein, 1865; Kleine, 1920*a*; Kramer, 1915; McGill, 1927; Marso, 1926; Martini, 1924; Musconi, 1924; Parker, 1924, 1929, 1930; Przibram, 1909, 1917, 1925; Robinet, 1850; Sacchi, 1921; Standfuss, 1894–95; Surcouf, 1922; Takahashi, 1912, 1912*a*; Titschak, 1925; Weissman, 1895; Wille, 1920.

(*f*) **Development at Varying Temperatures.**

Practically all experimental investigations of the effect of heat on the rate of development have been conducted with constant temperatures. No constant temperatures, however, exist in nature where insects are subject to continually varying temperatures owing to diurnal and seasonal fluctuations as well as to non-periodic changes in weather conditions.

Many authors have attempted to solve the difficulty of applying experimental data to actual outdoor conditions by considering the mean temperature as a true index of the conditions to which the insect is exposed in nature. There is, however, sufficient evidence to prove that this view is entirely erroneous.

Those insects, the development of which extends over the greater part of the year in temperate regions, are subjected during the course of development to a very wide range of temperatures. The influence of seasonal changes in the temperature on the development of hibernating or aestivating insects will be more conveniently discussed in a special section (see p. 104). Here we review only the available data on the action of varying temperatures on insects developing without a diapause.

There is nothing surprising in the fact that temporary exposures to temperatures above the medial range are usually injurious. The injury demonstrates itself in the more or less high percentage of mortality or in incomplete development. Janisch (1930) has expressed the opinion that short exposures to a high temperature retard the subsequent development at the optimum (see Table XI).

TABLE XI.

TIME OF DEVELOPMENT (IN HOURS) OF *PRODENIA LITURA* AT CONSTANT OPTIMUM TEMPERATURE, AND AT OPTIMUM AFTER AN EXPOSURE OF EGGS TO HIGH TEMPERATURE. (After Janisch.)

Stages.	At optimum 29–30°.	At optimum after an exposure to high temperature.			
		33° (56 hrs.).	35° (48 hrs.).	37° (35 hrs.).	40° (10 hrs.).
Hatching . .	45	—	—	16	64
1st moult . .	84	24	49	93	94
2nd moult . .	107	—	—	98	136
3rd moult . .	147	113	122	136	166
4th moult . .	180	64	169	167	207
5th moult . .	219	—	222	231	280
Pupation . .	303	—	312	376	383
Emergence . .	435	—	—	—	542

This table (Table XI) demonstrates that the exposure of eggs to a very high temperature (40°) retards development, but that the retarding action of exposures to temperatures ranging between 33–37° becomes perceptible only in the later stages, while the earlier stages develop more rapidly than under constant optimum conditions. The injurious effect of exposure thus does not become evident immediately. This is a very interesting and important fact, but more experimental data are wanted on this problem before any general conclusions can be drawn (see also Bolle, 1878; Bellati and Quajat, 1892).

The effects of temporary exposures to low temperatures on the subsequent development at the medial conditions are much better known. Duclaux (1869, 1876) observed long ago that exposure to cold stimulated the development of silkworm eggs. Acqua (1924, 1929) also stated that silkworm eggs should be preserved during the winter at a temperature of 3–4°. If the hibernation occurs at 14–15°, the eggs must be subjected to the action of cold in order to induce them to hatch (see also Zhmuidzinovich, 1892; Ishiwata, 1910, 1910*a*).

Of particular interest are the observations made by Bodine (1925) and Parker (1929, 1930) on the stimulating effect of low temperature on the development of grasshopper eggs. Their experiments demonstrated that if eggs were placed at 0° immediately after they had been laid and were later transferred to a favourable temperature, they always developed more rapidly than if placed directly at the latter temperature. This is illustrated by Table XII.

TABLE XII.

THE EFFECTS ON THE SUBSEQUENT DEVELOPMENT AT HIGHER TEMPERATURES OF AN EXPOSURE OF GRASSHOPPER EGGS TO 0°. (After Parker.)

Days at 0°.	Days taken for hatching at a favourable temperature.		
	27°.	32°.	37°.
0	26	32	46
30	25	31	37
60	23	29	31
120	20	21	17
180	17	18	15
240	16	12	11
500	15	10	10

The acceleration in the development caused by an exposure to low temperature was in proportion to the length of the exposure, up to 240 days. Longer exposures, up to 500 days, resulted in only a slight further acceleration.

In other experiments by Parker, grasshopper eggs were allowed to develop for varying periods of time at a favourable temperature, were then exposed to 0°, or to 8°, and were finally replaced in a favourable temperature until hatching. The results invariably showed an acceleration in the development apparently due to the action of cold. It is particularly significant that an exposure to 0°, other conditions being equal, resulted in a greater acceleration than an exposure to 8°. If we assume that even a very slight development takes place at 8° (which is below the developmental zero for the species), we should expect that the eggs exposed to 8° would hatch sooner than those exposed to 0°. Actually, however, exactly the opposite happens. The result can only be explained by the direct stimulation of the development by the low temperature.

Bodine (1925) suggested that the acceleration caused by cold depends on the exposure coinciding with a definite stage in the development of the egg. Parker's experiments led that author to the conclusion that the percentage of total development attained by the eggs before they are exposed to a low temperature has a direct relation to the degree of acceleration attained, *i.e.* the acceleration increased steadily up to the point when the eggs had gone through 32·6% of their total development before exposure.

Ludwig (1926) found that the rate of development of various stages of the beetle *Popillia japonica*, Newm., was affected by the fluctuation of the temperature. If the effective temperature was alternated with one above the optimum range, development was retarded, but an alternation with a low temperature had a definitely accelerating effect.

These data of Bodine, Parker and Ludwig do not agree with the observations made by Hase (1927, 1930) on the eggs of the flour moth, *Ephestia kuehniella*, Zell., and the bed-bug. This author has found that an exposure of eggs to a low temperature considerably delays their hatching in a favourable temperature as compared with eggs kept at a constant optimum temperature. Similar results are claimed by Janisch (1930) with regard to the development of *Prodenia litura*, F., and this author has put forward a theory that exposure to any temperature below the optimum invariably retards the development at a favourable temperature. That this theory cannot be considered universal is proved by the very different and absolutely reliable results obtained by Bodine, Parker and Ludwig.

These apparently contradictory conclusions can be reconciled with each other if we take into account that both Hase and Janisch experimented with insects very susceptible to low temperatures. It is only natural that in the case of such insects short exposures to low temperatures should result, apart from the retardation, in some obvious injuries and abnormal mortality. But grasshopper eggs used by Bodine and Parker did not show any injurious effects and the percentage of hatching was not affected by exposure to low temperatures. In other words, low temperature retards the subsequent development only if it is directly injurious to the organism, which is not always the case. If, however, the organism is not immediately injured by exposure to a low temperature, the latter may have a definitely accelerating effect on the development. This means that Janisch's (1930) theory of development being retarded even by the temporary action of non-optimal temperatures holds good in certain cases only.

The next problem in connection with the influence of varying temperatures on the development of insects is whether the fluctuations within the medial range have an effect different from that of the corresponding constant temperatures. One aspect of this problem was discussed twenty years ago by Sanderson (1910), who pointed out that in the case of fluctuating temperatures it is incorrect to use the mean temperature for the calculation of the thermal constant, since the developmental value of one degree is not constant, but depends on the temperature. Sanderson emphasised, therefore, the necessity of studying the rate of development at a series of controlled temperatures in order to obtain values for each temperature. When studying development at fluctuating temperatures, periods spent at each temperature must be evaluated separately.

Another side of the same problem is seen in the effect of fluctuations on the rate of development. Headlee (1914) studied the development of the grain aphis, *Toxoptera graminum*, Rond., at constant and at fluctuating temperatures and found that the constant temperature is more effective than a fluctuating one with the same average. Aphids at a constant temperature of 26·6° reached maturity in 6 days, instead of in 8 at the fluctuating temperature, and the daily rate of reproduction increased more than twice. It must be noted, however, that the aphids lived 25 times as long at the fluctuating temperature as they did at the constant one. It would appear that the total productivity was lower at the constant temperature. Similar data were obtained by the same author (Headlee, 1929) in his experiments with pupae of the codling moth which required eight days less for their development at a constant temperature of 17·22° than under a diurnal fluctuation varying from 10° to 24·44°.

The larvae of the wax moth, *Galleria melonella*, L., in the experiments of Destouches (1921) developed at the same rate at alternating and at constant temperatures. The life of adult moths, however, was very much longer at alternating temperatures than at the constant (30–35 days instead of 5), and the total productivity of one pair was increased from 15 to 25–35 eggs per pair by the fluctuation of the temperature.

While the results reviewed above do not suggest that there is a stimulation caused by fluctuations of the temperature, some later and more careful investigations favour a different conclusion. Peairs (1927) obtained a definite, if not very great, acceleration in the development of blowfly larvae at temperatures changed at 6–12 hour intervals. His results are given in Table XIII.

TABLE XIII.

Development of Blowfly Larvae at Fluctuating Temperatures. (After Peairs.)

Temperatures for 6-hour periods.				Average temperature.	Accumulated temperature.	Deviation from the thermal constant.
1.	2.	3.	4.			
20°	25°	20°	15°	20°	92·4°	−12·3°
10	20	30	20	20	95·2	− 9·5
10	30	30	20	20	98·0	− 6·7
5	25	25	20	20	95·2	− 9·5
15	25	25	20	20	96·6	− 8·1
15	25	35	25	25	101·6	− 3·1
20	25	30	25	25	104·5	− 0·2

Although the deviation was often less than the individual variation in the case of constant temperatures, it is significant that it was always negative, *i.e.* it invariably indicated an acceleration in development.

Cook (1927) while studying the development of the cutworm, *Porosagrotis orthogonia*, Morr., also reached the conclusion that fluctuations in the temperature have a definitely accelerating effect on development, as well as on the rate of CO_2 production.

Shelford (1927, 1929) concluded from his extensive studies on the development of the codling moth under actual weather conditions that the effect of normal daily fluctuations of outdoor temperatures amounts to 7–8% more rapid development than under constant temperatures. Sharp fluctuations, however, may slightly retard development.

Very interesting data were obtained by Parker (1929, 1930) on grasshoppers. Eggs collected in the field hatched at a constant temperature of 32° after 5 days, while those kept for 16 hours daily at 12° and for 8 hours at 32° developed in three days, *i.e.* there was an increase of 66% in the rate of development. When eggs were kept at alternating temperatures, viz. 27°, 32° and 37° for 8 hours and at 22° for 16 hours, development at any of the two alternating temperatures was more rapid than at the corresponding high temperature. Very similar results were obtained for the development of the larvae (see Fig. 29, p. 91). In both cases the greatest acceleration was produced when an effective temperature alternated with a temperature below the zero of development, *i.e.* 12°, while the alternation of two effective temperatures produced less acceleration. However, if the two alternating temperatures were separated by an interval of 10°, or of 20°, the development showed no acceleration as compared with that at the corresponding mean temperature, providing the daily exposure to the lower temperature was twice the exposure to the higher temperature.

It is too early to attempt to draw any very definite conclusions from the evidence summed up above. One point, however, is beyond dispute, namely, that fluctuations of temperature are not without an effect on the rate of development. This effect is often positive, particularly when a favourable temperature alternates with one below the zero of development (but not low enough to be injurious), while an alternation with high temperature is usually harmful. In any case, the impossibility of using average temperatures in the exact estimation of the influence of actual weather conditions on the development of insects is abundantly clear.

(*g*) **The Course of Development.**

While heat has a definite effect on the rate of development as has been shown above, it affects its course also by influencing in a certain way the development of the whole organism, or of its parts. A brief review of such influences is presented below.

(i) *Size.*

Some entomologists experimenting with the influence of low temperatures on caterpillars have obtained adults of less than normal size, but Titschak (1925, 1927) explains all such results by the inexactness of the experiments. His own investigations on the clothes moth, *Tineola biselliella*, Hum., demonstrated that at lower temperatures larger and heavier moths were produced (Table XIV).

TABLE XIV.

WEIGHT OF ADULTS OF CLOTHES MOTH BRED AT DIFFERENT TEMPERATURES. (After Titschak.)

Temperature.	Average weight in grams.	
	Males.	Females.
30	2·06	4·18
25	2·16	5·06
20	3·02	5·53
15	3·62	5·90

This increase in size at low temperatures may perhaps be explained by the fact that exposure to such temperatures lengthens the larval life and the total amount of food taken by the larva, while the percentage of food absorbed and utilised for building up the tissues is greater than at the higher temperatures. These are not theoretical considerations, but the result of very exact experiments by Titschak.

Similar conclusions as to lower temperatures producing insects of larger size have been reached by a number of other investigators, *e.g.* by Schlöttke (1926) in the case of *Habrobracon juglandis*, Say, by Musconi (1924) with *Calliphora erythrocephala*, Mg., by Dewitz (1913) with *Porthetria dispar*, L., by Alpatov and Pearl (1929) with *Drosophila melanogaster*, Mg., and by Standfuss (1896) with various species of Lepidoptera. The last-named author found that by the application of a high temperature the larval period of *Lasiocampa quercifolia*, L., can be shortened from the normal 22–26 to 7–12 weeks, and that extremely small adults are obtained. He explained the results by the reduction in the total amount of food taken by the caterpillars under these conditions. (See also p. 92.)

(ii) *Moults.*

The general influence of changes in temperature on the mechanism of moulting has not been studied, but Pictet (1918*a*, 1918*b*) has recorded some observations on the influence of temperature on the emergence of Lepidoptera from the pupae. According to his data, a sudden rise in the temperature is favourable for emergence and he explains this on mechanical grounds, viz. the expansion of the body at a high temperature and the consequent rupture of the pupal integument. Neither the observations nor their explanation appear very convincing.

The available information on the relation between the temperature conditions and the number of moults is both scanty and contradictory.

Several authors have obtained results indicating that a relatively high temperature increases the number of larval stages and moults. Thus, Kreyenbergh (1928) found that the larvae of two species of *Dermestes* bred at 28° had five moults in the case of males, and six in the case of females, instead of four and five, respectively. Larvae of *Sphodromantis viridis*, Forsk., in Przibram's (1909) experiments had 8–9 moults at 25° and 9–11 at 37°. Similar results were obtained by Severin and Severin (1913) with the stick-insect, *Diapheromera femorata*, Say.

The hoppers of *Melanoplus mexicanus*, Sauss., on the contrary, moulted six times at 22–27°, and only five times at 32–37° (Parker, 1929, 1930). A lower temperature in this case increased the number of larval stages and of moults. Lengerken (1925) studied the effect of low temperature on the development of *Tenebrio molitor*, L., kept in a cool cellar (exact temperature not stated). The length of the life of the larvae was increased by several months, and there were many supernumerary moults. These did not occur in a normal way, and the majority of the resulting pupae and adults were teratological.

Still further uncertainty was introduced into the problem by Titschak (1926), who reached the conclusion that in the larvae of the clothes moth the number of moults does not depend on the temperature. This author criticised the different results obtained by others and explained them by the lack of adequate observations. His own conclusions were based on a very long series of experiments and do not give rise to any doubt as to their being correct for this particular insect, but it would not be safe to generalise until more work is done on the problem.

Another interesting point with regard to moults as affected by temperatures was revealed by the work of Janisch (1930) on the caterpillars of *Prodenia litura*, F. While the different stages are normally easily separated by their colour and pattern, two different stages were often identical in colour in the case of caterpillars subjected temporarily to a high temperature, some characters of a later stage appearing in the earlier ones. Janisch explains this by a partial premature development caused by the high temperature.

(iii) *Chitinous structures.*

The influence of temperature on the development of wings in insects has been studied chiefly in Aphids. In these insects, however, the problem is very complicated since the winged forms represent, at the same time, the sexual generation, while the wingless ones are mainly agamic. We return to this problem of alternation of generations, as affected by external factors, in a later section (see p. 113).

Definitely short-winged (brachypterous) and long-winged (macropterous) forms are known in many insects (Hemiptera and Orthoptera), but so far no work has been done on these in connection with the temperature conditions of development, and the few available data refer to the relative length of wings in fully winged insects under different temperature conditions. Most of these data are the result of very inexact experiments aiming at the production of "interesting" aberrations, and these it is not proposed to review here. More serious, though not sufficiently extensive, investigations on the problem were undertaken by Dewitz (1902, 1912*a*, 1920), who obtained wingless or short-winged adults of bees, wasps and flies by applying a low temperature (ice chamber) to the pupae. Since the same results can be obtained by depriving the pupae of oxygen, the author suggests that a low temperature prevents the oxidation processes necessary for normal development. Michailov (1927) studied the relative length of wings in bees incubated at 30° and at 35° and found that the bees subjected to a lower temperature had shorter wings. Nadler (1926) investigated the effects of temperature on the length of vestigial wings in *Drosophila virilis.* The length proved to vary with the changes in temperature in accordance with van't Hoff's rule.

The results obtained by Michailov and Nadler do not contradict those of Dewitz, since the latter considered that the action of very low temperatures interfered with the normal metabolism, while the other two authors experimented within the favourable temperature range. (See also Kusnezov, 1929.)

Temperature may affect not only the length of wings, but also their structure. For example, considerable modifications of the wing-venation in tsetse flies occur as a result of high temperatures acting on pupae (Roubaud, 1909), and in *Vanessa urticae*, L., as the result of a low temperature, between 7 and 9°, on the larvae (Jachontov, 1906). C. Stern (1927) described a mutant of *Drosophila* with recurved wings obtained by the action of temperatures above 20–22° on freshly emerged flies, but this should be more properly classed as a teratological case.

The time of the appearance of wings in the course of post-embryonic development may be altered by abnormal temperature conditions, since in *Tenebrio molitor* rudimentary wings appear even in the larval stage, if the larvae are kept at a temperature of 29·5° (Singh-Pruthi, 1924). This must be due, on the one hand, to the prolongation of larval life occurring at such high temperatures, and, on the other, to the direct effect of the temperature.

Scales on the wings, as well as on the body, of Lepidoptera may not develop fully when either high, or low, temperatures are applied during the development of the insect (Federley, 1905; Emeljanoff, 1924; Kosminsky, 1909, 1911).

Variations in the chitinous structures other than the wings, caused by temperature, may be considerable and are at present known to affect the legs, antennae, palpi, head, thorax, endoskeleton, etc. (Kosminsky, 1909, 1911, 1912, 1923; Emeljanoff, 1924; Michailov, 1927; Hoge, 1915). The size of the eyes (Hyde, 1922) and the number of the facets in the compound eyes of adult *Drosophila* vary inversely with the temperature, to which the larvae are subjected. With each ten degrees drop in the temperature between 29° and 15°, the number of facets increases on the average 2·6 times in the males and 3·5 times in the females (A. Hersch, 1924; R. Hersch, 1924; also Krafka, 1920; Seyster, 1910; Zeleny, 1925, 1928).

(iv) *Sex.*

Of special interest are the observations on the influence of temperature on the genital system, *i.e.* on its structure. (Its influence on its functions is discussed elsewhere, see p. 92.)

Kosminsky has described the modifications in the copulatory apparatus of moths under the influence of both moderately low (10–11°) and moderately high (30°) temperatures. The modification in the males was in the direction of the females and *vice versa*, so that intersexes can be produced in this way with intermediate external characters (antennae, coloration, etc.) (see also Emeljanoff, 1924; Goldschmidt, 1922). Golowinskaja (1927, 1927*a*) proved that such partial intersex characters, produced by the action of low temperatures, are inheritable, which means that the temperature affects the genital cells of the original female. The possibility of the temperature affecting the genital cells is further suggested by the work of Plough (1917, 1921), who has recorded a decided increase in the percentage of crossing-over amongst the offspring of *Drosophila* subjected during their post-embryonic development to temperatures of 13° and of 31°.

(v) *Blood.*

The influence of heat on the body fluid of insects has been investigated by Dewitz (1912, 1913). A discoloration of blood becomes noticeable at temperatures not higher than 40°. An exposure to this temperature for forty minutes may be not fatal to some insects, but it is questionable whether it has no after-effects (see also L. Ackerman, 1926).

(vi) *Coloration.*

The literature on the effect of different temperatures on the coloration of insects, particularly of Lepidoptera, is enormous, and it is not proposed to review it here, or even to list it fully in the bibliography, since the bulk of the papers simply present the results of more or less crude " experiments " designed with a view to obtaining " new " aberrations. It would be unwise, however, to regard all work done on the subject as valueless scientifically. It is true that most of the authors paid attention only to the obvious effects of temperature on the colour and pattern of the wings of Lepidoptera, but these characters, while in themselves physiologically unimportant, must be regarded as external indices of some metabolic processes.* From this point of view, temperature experiments with Lepidoptera present a definite interest, and a brief survey of the relatively few theoretical papers will be not out of place. (For more exhaustive reviews see Bachmetjew, 1907; Prochnow, 1926–1927.)

Weismann (1875, 1895) worked mainly with seasonally dimorphic species of Lepidoptera, and his conclusions were somewhat indefinite. He laid considerable stress upon the constitutional tendency of the colour and pattern to vary in a definite direction, the external factors (*e.g.* the temperature) merely supplying the initial stimulus. On the other hand, he admitted the possibility of a direct influence of temperature on the chemical constitution of pigments.

Urech (1898) attempted to explain on physiological grounds the production of colour aberrations by the application of abnormal temperatures. He suggested that a pupa placed in a cold environment gives out heat. The loss of heat must be compensated, and this is done at the expense of some internal chemical processes, mainly oxidation of the hydrogen of blood and of pigments.

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* See my review on the pigments in insects (1928, *Trans. Ent. Soc. Lond.*, **76**: 286–288).

In this way certain chemical compounds rich in carbon are formed. They are mostly dark in colour and represent dark pigments. On the other hand, high temperatures may directly increase the rate of oxidising processes, and the result is again a dark pigment.

The theories offered by Standfuss (1896) and Fischer (1896, 1897, 1900, 1903) are more or less similar. The second of these authors illustrated his ideas by the following table (Table XV) of the temperature aberrations of several species of *Vanessa*, etc.

TABLE XV.

ABERRATIONS OF *VANESSA*, ETC., PRODUCED BY DIFFERENT TEMPERATURES.
(After Fischer.)

Extreme cold, 0° to −10°.	Moderate cold, 0° to 10°.	Normal form.	Moderate heat, 36° to 41°.	Extreme heat, 42° to 46°.
ichnusoides	*polaris*	*Vanessa urticae*	*polaris*	*ichnusoides*
antigone	*fischeri*	*Vanessa io*	*fischeri*	*antigone*
testudo	*dixeyi*	*Vanessa polychloros*	*dixeyi*	*testudo*
hygiaea	*artemis*	*Vanessa antiopa*	*artemis*	*hygiaea*
elymi	*wiscotti*	*Pyrameis cardui*	*wiscotti*	*elymi*
klymene	*merrifieldi*	*Pyrameis atalanta*	*merrifieldi*	*klymene*
weismanni	*porima*	*Araschnia prorsa*	*porima*	*weismanni*

It is obvious from this table (Table XV) that the action of temperature is not specific, but is due to the inhibition of normal development by abnormal conditions. The correctness of this view is supported by Fischer's experiments in which colour aberrations, identical with those produced by heat and cold, were obtained by subjecting pupae to narcotics. Fischer's theory of inhibition is accepted by Hering (1926), while Schuckmann (1909) partly corroborated it by comparative histological studies of various organs of normal pupae and of those subjected to a temperature of −8°. These studies proved that low temperatures actually bring metabolic processes to a standstill.

Schröder (1903) evolved a theory according to which dark pigments are formed under the influence of cold as a means of increasing the absorption of heat by the insect and thus counterbalancing the effects of the cold on development. No experimental evidence in support of this interesting view was, however, given.

An attempt to study separately the effects of temperature on different pigments was made by Linden (1902, 1904), who, like Urech (*l.c.*) insisted on the importance of the rate of oxidation in the formation of pigments. She concluded that red pigments are affected by the temperature directly and the black ones indirectly.

A very thorough, if somewhat too theoretical, discussion of all the known facts and hypotheses relating to the influence of the temperature on coloration of Lepidoptera led Bachmetjew (1907) to the following conclusions. In the case of extreme temperatures there are four possible explanations of the mechanism of variation, viz. :—

(1) The circulation of blood may be inhibited and this may affect the distribution of pigments.

(2) At high temperatures the metabolism may increase.

(3) The protoplasm of cells in the wings may lose its ability to concentrate

the colouring matter from the blood, owing to a state of torpor induced by extreme temperatures.

(4) The colouring matter itself may be altered chemically or even not be formed.

With reference to medial temperatures Bachmetjew believed that they cannot exert a direct influence on the chemistry of pigments. Neither did he consider that they act by altering the rate of metabolism, but rather by affecting the rate of movement of protoplasm in the cells. This suggestion, however, is not made sufficiently clear, or convincing.

Przibram (1919) followed Urech and Linden in connecting the building up of pigments with the rate of oxygen intake, while he believed that the colour aberrations produced by extreme temperatures are due to the destruction of the respective pigments.

Prochnow (1914) specially stressed the point, already noted by other authors (*e.g.* by Merrifield, 1890, 1892, 1894), that aberrations can be produced only if the pupae are subjected to different temperatures at a definite stage in their development. Thus, it becomes imperative to evaluate the periods of development, and for this purpose the rate of development must be expressed in developmental units (see p. 23).

The latest important work on the subject is that by Giersberg (1929), who has expressed the opinion that the alterations in the colour and pattern of Lepidoptera produced by temperature must be due to the unequal velocity of development of different parts and of different substances.

Compared with the literature on the coloration of Lepidoptera, the number of papers dealing with other insects is very small. Several authors have studied the influence of temperature on the black pigmentation, and in most cases they found that the black pigments (probably melanines) developed best at low temperatures, while high temperatures produced pale-coloured forms (Genieys, 1925; Knight, 1924; Schlöttke, 1926; Kühn and Henke, 1929). This suggests that black pigment is not due to the increased metabolism, but that, on the contrary, the substances, which at low temperatures are deposited as black pigment, at high temperatures are consumed, or are otherwise disposed of. In some cases, however, the formation of black pigment is favoured by high temperatures, *e.g.* in the hoppers of locusts (Nikolsky, 1925) and in those of the stick-insect, *Carausius morosus*, Br. W. (Toumanoff, 1926). These cases, however, refer to the rate of the blackening of larvae after moults, and not to the total increase, or decrease, in the black pigment. The process involved is clearly that of oxidation, accelerated by high temperature.

Very detailed experimental investigations in the conditions of development of black pigment in the bug *Pyrrhocoris apterus*, L., carried out by Henke (1924) confirmed this latter view. This author stressed the idea that the influence of heat on pigmentation is not direct, but is exercised through the acceleration of general metabolic processes and in particular of the circulation caused by heat.

(*h*) **Respiration.**

The fact that heat exerts some influence on the rate of respiration in insects was known a century ago to Treviranus (1831). Apparently the first quantitative studies of this interrelation were those of Bütschli (1874), who found that in the case of a cockroach a rise in the temperature was followed by a regular increase in the gaseous exchange. At 15° the exchange was double that at 4°, and at 32° it was seventeen times that at 3°.

A number of authors have determined quantitatively the connection between the temperature and the CO_2 production in insects, without formulating any rules governing the phenomenon (Luciani and Piutti, 1888; Vernon, 1897; Batelli and Stern, 1913; Ellinger, 1916; Holmquist, 1928).

The essentially chemical character of the processes involved naturally led to attempts to apply chemical laws for their explanation. Parhon (1909) and Tangl (1909) when studying the carbon dioxide production by flies obtained figures in close agreement with van't Hoff's rule, but the data obtained by other investigators (Bodine, 1921, 1923; Buddenbrock, 1928; Buddenbrock and Rohr, 1922*a*; Dirken, 1922) did not follow the rule. An agreement with the Arrhenius equation has been found in the case of the oxygen consumption by the pupae of *Drosophila* (Orr, 1925) and by grasshopper nymphs (Rogers, 1928, 1929).

Krogh (1914–1914*c*, 1916) studied the CO_2 production by the pupae of *Tenebrio molitor*, L., with the help of a specially constructed micro-respiration apparatus. The resulting curve of the temperature relations was a straight line between 18° and 28°, an upward bending curve at temperatures above 28° and a downward bending one at temperatures below 18°. Krogh's conclusions were criticised by several authors, more particularly by Shelford (1929).

While all the authors mentioned above studied the gaseous exchange as if it were a simple chemical process, some evidence has accumulated to show that this is far from being the case. Thus, Slowtzoff (1909) observed that CO_2 production in the beetle *Geotrupes stercorarius*, L., increased with the air temperatures, but that within certain limits, viz. 12–24°, the rate remained stationary. The maximum rate is reached at 48°, after which it falls rapidly. The studies of Walling (1906), Dirken (1922), Hazelhoff (1926; see H. Jordan, 1927), Lee (1925), and Crozier and Stier (1925) indicated clearly that there may be a serious source of error. It is overlooked that the rate of respiration of insects depends not only on the rate of the gaseous metabolism within the organism, but also on the activity of the respiratory organs, since the rate of respiratory movements, the opening and closing of spiracles, etc., undoubtedly depend on the temperature. This activity is influenced by the temperature quite independently of the rate of metabolism, while the measurements of the CO_2 production, or of oxygen consumption, show only the total results of several complicated processes and cannot be expected to present a strict regularity. This point of view has recently been stressed by Buddenbrock (1928; see also Buddenbrock and Rohr, 1922, 1922*a*), who has pointed out that an increase in the temperature has a double action, viz. (1) a direct effect on the rate of metabolism, and (2) an effect on the nervous system with resulting movements which not only affect the rate of gaseous exchange but also cause the body temperature to rise considerably. It is necessary, therefore, to study separately the effects of temperature on active insects, and on insects in an inactive state, *e.g.* under narcotics, or in the pupal stage, though some pupae exhibit considerable movements which cannot fail to affect the results.

Another source of error lies in the fact that the rate of gaseous metabolism varies for internal reasons during the life of a stage. Thus, in the pupae of *Tenebrio* kept at a constant temperature the CO_2 production decreases gradually during the first four-fifths of the pupal period and then increases rapidly (Fig. 9; Krogh, 1914*a*, 1916; Shelford, 1929). Still more complicated relations were found by Heller (1925, 1930) in the pupae of moths. It is imperative, therefore, to compare the rates of gaseous exchange at different temperatures in the insects of exactly the same stage of development.

The rate of metabolic response to temperature depends, further, on the length of exposure. Sayle (1928) working with dragonfly nymphs observed that the CO_2 output increased after 24 hours' exposure to a higher temperature, but decreased again at a longer exposure. This must also be taken into account when exact results are required.

A very interesting attempt to throw some light on this problem has recently been made by Heller (1925, 1928, 1930). This author, after a long series of experiments on lepidopterous pupae, reached the conclusion that the relation of the oxygen consumption to temperature can be best expressed by three straight-line curves (Fig. 10) characterised by the points where they cross the temperature axis. For the first curve this point lies between 0° and $-7°$, and this curve represents the processes of the basal, or subsistence, metabolism. The second curve crosses the axis at 9° and represents the sum of the basal metabolism and of the metabolic processes occurring during quiescence (*i.e.* during the latent development). The third curve represents the sum of three phenomena comprising, not only the basal metabolism and that of the latent development, but also the processes that go on during the active (subitane) development. The point at which the third curve intersects the temperature axis has no biological meaning. However, the point where this curve crosses the second one, near 20°, represents the temperature above which quiescence is interrupted and active metabolism becomes possible. The common formula of all three curves is :

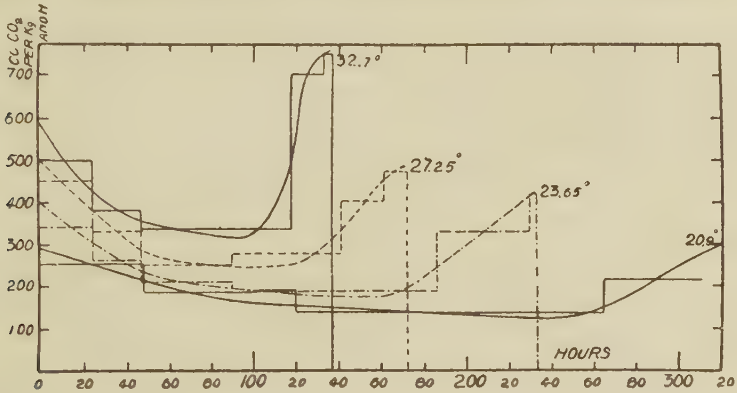

FIG. 9.—Graph showing the variation in the rate of CO_2 production during the pupal life of *Tenebrio* at different temperatures. (After Shelford, 1929.)

$$\frac{I}{V}(T-K)=C$$

where V represents the oxygen consumption in cubic centimetres, per one kilogram in one hour, K, the point at which the line crosses the temperature axis, T, the temperature, and C, a constant which for a given stage of the insect has the same value for all temperatures within the curve.

The formula of Heller is very similar to that of Blunck (see p. 22) and the value of K has been found experimentally to be the same as in Blunck's formula, *i.e.* it represents the temperature above which metabolism becomes possible.

Several authors (Krogh, 1914*b*; Tangl, 1909; Peairs, 1927; Shelford, 1929) have obtained data indicating that the total amount of CO_2 produced during the development is constant for the stage (see Table XVI).

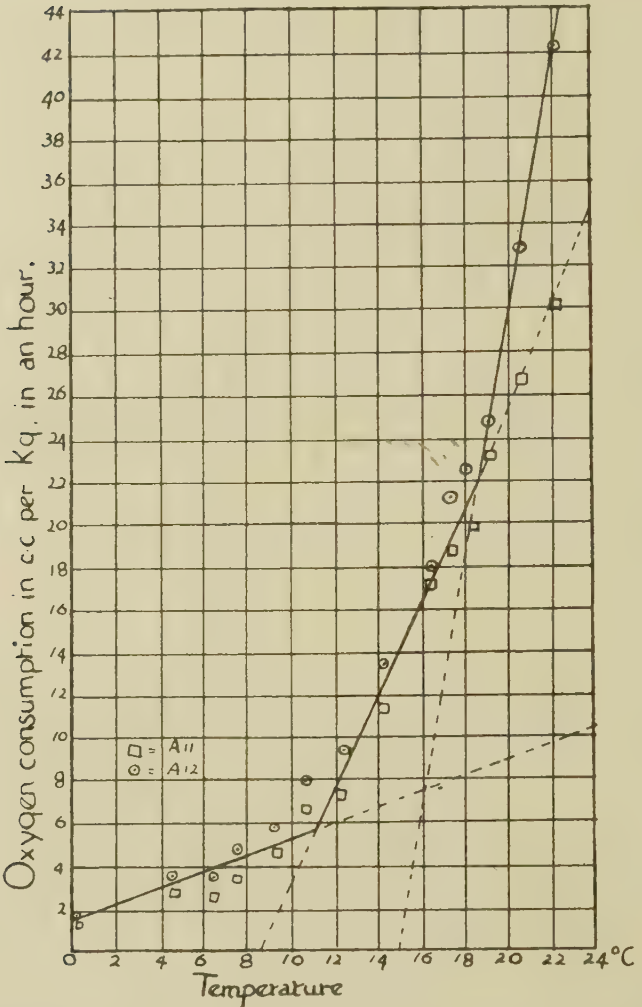

Fig. 10.—Three straight-line curves representing the oxygen consumption by lepidopterous pupae in relation to the temperature. (Re-drawn after Heller, 1930.)

TABLE XVI.

Total CO_2 Produced by *Tenebrio molitor* during Pupal Development.

Temperature.	CO_2 produced, in litres per kilogram.
32·70	59·30
27·25	58·00
23·65	59·10
20·90	59·60
Average	59·00

This observation, as well as the agreement between the data of Heller and Blunck, suggest that the rate of gaseous metabolism may be regarded as a good index to the sum-total of developmental processes. Viewed from this angle the gaseous metabolism, instead of representing only a special problem of the physiology of respiration, becomes a means of exact studies in the development generally. It is necessary to stress this point since there is a tendency amongst entomologists to regard investigations of this kind as belonging rather to the field of pure physiology and as bearing no immediate relation to more general and practical problems.

The upper temperature limit of respiration has been studied by Potonié (1924), who arrived at the following conclusions. As long as an insect is alive and healthy, and uninjured by a high temperature, its oxygen consumption follows van't Hoff's rule. When the temperature reaches a point at which an exhaustion of tissues begins, the oxygen consumption sinks rapidly. The turning point is due, therefore, to the destruction of metabolic enzymes (Duclaux, 1899) and to the exhaustion of the tissue.

(*i*) **Circulation.**

The available data on the influence of temperature on the rate of circulation are very meagre. Crozier and Federighi (1925, 1925*a*) and Koizumi (1928) studied the frequency of heart-beat in the silkworm as affected by heat and reached the conclusion that the relation is exactly in accordance with van't Hoff's rule. Fries (1926) found that the frequency of pulsation of the heart in the larvae of *Blatta orientalis*, L., increases with the temperature in accordance with the Arrhenius equation.

(*j*) **Reproduction.**

Any external factor may influence the fertility of an insect in two different ways. Firstly, it may affect the rate of development of the gonads in the insect body. Secondly, the mechanism by which the mature eggs are deposited may also be directly influenced. While theoretically the first point appears to be of more importance, it should be pointed out that sufficient attention has not been paid to an exact analysis of the physiological effects on fertility of temperature, or other factors.

Sufficiently exact experimental data on the length of the pre-oviposition period, which corresponds more or less to the period of the maturation of the gonads, are not numerous. The work of Bishopp, Dove and Parman (1915) on the house-fly may be quoted, as an example of the influence of heat on the rate of maturation of the gonads. These authors found that the length of the pre-oviposition period may vary from four days at 30·6° to twenty days at 20°. Wille (1920) records some observations on *Blattella germanica*, L., in which a low temperature of 10° doubled the time between copulation and the formation of egg-capsules.

Our present knowledge on the temperature range of reproduction in insects is not much more extensive. With regard to the tsetse fly (*Glossina palpalis*, R.-D.), Roubaud (1909) stated that reproduction is possible only between 25° and 30°, *i.e.* that the whole range is only about 5°, but in this particular species the range of all activities is very narrow. No reliable data appear to exist on the range of reproductive activities in other insects, although there is some information available on the inhibiting effects of the temperatures above and below the optimum. Mayne (1926) studied the influence of temperature on the fertility of the mosquito *Anopheles quadrimaculatus*, Say, and found that the eggs are laid at 12·8–16·7°, but not at 4·4–12·2°. One set of gravid females was divided into two lots, each containing ten individuals. One lot was kept at the room temperature, 17·2–25·5°, and produced 384 eggs with 100% fertility. Another lot, kept at 4·4–12·2° for 17 days and then exposed to the room temperature for four days, laid 292 eggs with 35% fertility. This observation proves that even a temporary exposure to a moderately low temperature may reduce both the number of eggs per female, and their fertility. In Voelkel's (1924) experiments, exposures of the males of the khapra beetle, *Trogoderma granarium*, Everts, to a temperature of from −8° to −10° for 3–4 hours did not affect their reproductive ability, although the percentage of infertile eggs in their progeny increased slightly. The males kept at −8° for over 30 hours did not produce any progeny. In the case of the louse, *Pediculus vestimenti*, L., Sikora (1915) has found that no eggs are produced at temperatures under 25°, while a cooling to 16° for two hours is sufficient to reduce the number of eggs laid. The temperature limits of these insects are generally very high. Pospelov's studies (1925, 1926) on the maturation of sexual products in *Locusta migratoria*, L., showed that, while they matured within a month if kept at a constant temperature of 35–38°, the specimens kept at temperatures alternating between 30° during the day and 20° at night developed very slowly and died without laying eggs. It will be seen from these examples, that even temperatures which can hardly be called low in the usual sense of the word, may produce very serious inhibiting effects on the developing gonads.

It is also known that the sexual development may be inhibited by high temperatures. Young and Plough (1926) subjected *Drosophila* to a temperature of 32°, with the result that 96% of the males were rendered sterile while only 50% of the females were affected in that way. It is interesting to note that the effect on males was not permanent, but lasted only as long as the high temperature was maintained, most of them recovering their normal fertility when placed again in an optimum temperature. Exposures to 31° for over ten days increased greatly the number of flies which were permanently sterilised (see also Strauss, 1925). The problem of the sterilisation of Lepidoptera by high temperatures formed the subject of special investigations by Pospelov (1911), who studied the effects on the fertility of adults of high temperature acting on the pupae. The results of his numerous experiments, supplemented by exhaustive histological studies, suggest that a moderate increase in the temperature applied to pupae affects different species in different ways. In some species, *e.g.* in *Euxoa segetum*, Schiff., the pupal stage is shortened and sexually immature adults emerge before their normal time. At a low temperature, the pupal stage is longer and the ovaries mature before the emergence takes place. In other species, *e.g. Aporia crataegi*, L., the pupal period is also shortened by a high temperature, but the emerging adults are sexually mature. Sexually immature adults are produced only at very high temperatures (47°) and their immaturity is due to the heat torpor. In the majority of species, high temperatures do not affect the degree of development of the ovaries, this being a fixed hereditary character. Data obtained by Znamenskiĭ (1915) tend to show that even in the case of adults emerging at high temperatures with undeveloped ovaries, this abnormality is of little importance, since it disappears in the course of further development. On the other hand, Znamenskiĭ obtained results showing that a low temperature (19°) acting on pupae produces adults with both the ovaries and the fat body poorly developed.

An explanation of the inhibition of the development of ovaries in Lepidoptera by high temperatures has been offered by Enderlein (1902). He suggests that this is due to the fact that the ovaries are formed only towards the end of the pupal stage. When the development is too rapid owing to a high temperature, the adult may be completely formed and emerge before the ovaries are developed.

The influence of temperature on the rate of reproduction in insects has been studied by a number of authors, but only a few examples are quoted here. Schubert (1928) kept 20 males and 20 females of the bug *Piesma quadratum*, Fieb., for ten days and obtained the following numbers of eggs at different temperatures (Table XVII).

TABLE XVII.

NUMBERS OF EGGS LAID BY 20 PAIRS OF *PIESMA QUADRATUM*, FIEB., IN TEN DAYS, AT DIFFERENT TEMPERATURES. (After Schubert, 1928.)

Temperature.	Numbers of eggs.
3– 6°	0
10–12	136
18–20	352
37–40	764

The increase in the reproductive ability of the Chalcid *Trichogramma evanescens*, Wstw., in relation to the increase in the temperature is illustrated by the curve in Fig. 11 (Schulze, 1926). This curve indicates a rapid decrease in the rate of reproduction at the temperatures near the upper limit.

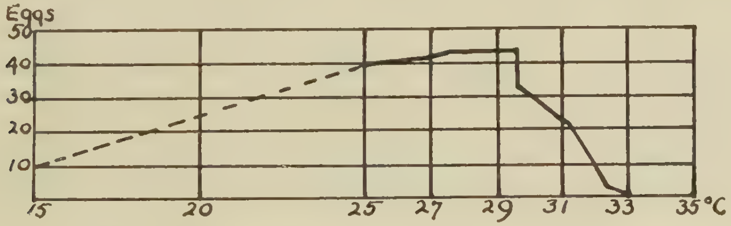

FIG. 11.—The influence of temperature on the total number of eggs laid by *Trichogramma evanescens*, Wstw. (Re-drawn after Schulze, 1926.)

In the case of viviparous Aphids, the rate of reproduction is also fundamentally affected by heat. In *Aphis avenae*, F., in Ewing's (1916) experiments the average rate at 15·5° was 2·2 births per day, per individual. At 26·6° the rate was 6·1 and at 32·2° it fell to 0·25. (See also Troitskiĭ, 1929.)

Bliss (1927) is apparently the only author who has attempted to differentiate between the influence of temperature on the development of gonads, and on the actual oviposition. When studying the correlation between the number of eggs laid by grape leaf-hoppers and the average temperature on that and the preceding day, he arrived at the conclusion that it was the latter which governed the rate of oviposition. This means, that the effect of heat upon the rate of development of eggs is of greater importance than its effect upon the egg-laying.

Although a higher temperature stimulates the production of eggs, it also shortens the individual life of the insect, so that the total number of eggs produced is not necessarily increased by raising the temperature. In Titschak's

(1925) experiments on the clothes moth, females lived 19 days at 20° and laid 94·9 eggs, while at 30° they lived six days and laid 79 eggs. The total progeny at a higher temperature was in this case less than at a lower one.

Kühn and Henke (1929) found that a continuous breeding of *Ephestia kuehniella*, Zell., at 25° resulted in a reduction in the average number of progeny. On the culture being transferred to a more moderate temperature, the normal productivity did not return immediately, but only in the course of several generations.

While the above cases illustrate the direct effect of heat upon the development of gonads in an adult insect, Eidmann (1929) has published an interesting preliminary communication on his temperature experiments with the pupae of Lepidoptera. The results show that adults bred from pupae kept at a low temperature produce less eggs than those emerging from pupae kept at a high temperature. Thus, the fertility of an insect may be affected by the influence of heat on the early stages.

That temperature conditions may affect the type of reproduction in an insect is evidenced by Wasmann's (1891) data that the breeding of ants at artificially raised temperatures (degree not stated) resulted in the workers producing parthenogenetic eggs.

A brief summary of the literature on the oviposition of insects in relation to temperature was published by C. Robinson, 1925.

(*k*) **Duration of Life.**

The fact that within the favourable range of temperature the individual life of an insect becomes longer at lower temperatures is well known.

For example, the normal length of life of adults of *Dendrolimus pini*, L., *Lasiocampa quercus*, L., and *Porthetria dispar*, L., is about 9–10 days, but at temperatures ranging from —4° to 22° they survive for as long as 51 days (Pictet, 1913*a*).

Baumberger (1914) has conducted numerous experiments and has published a table showing the length of the adult life of various insects at three different temperatures (Table XVIII).

TABLE XVIII.

LONGEVITY OF ADULT INSECTS AT DIFFERENT TEMPERATURES. (After Baumberger.)

Order.	Temperature.								
	High (22·22°).			Medium (16·66°).			Low (5·55°).		
	Longevity in days.								
	Max.	Aver.	Min.	Max.	Aver.	Min.	Max.	Aver.	Min.
Coleoptera . .	7	5·8	1	7	7	5	39	24·6	1
Hymenoptera .	15	5·2	1	8	5	3	15	7·3	1
Diptera . . .	7	1·6	1	15	2·5	1	27	4	1

Similar observations and isolated facts have been recorded by many other authors (*e.g.* Cleghorn, 1919; V. Engelhardt, 1915; Gauthier and Raybaud, 1909;

Hase, 1919; Teissier, 1928; Titschak, 1926*a*; Zhmuidzinovitch, 1891; etc.), but only very few of them attempted to study the phenomenon in a systematic way. Baumberger (*l.c.*) reached the conclusion that the increase in the length of the adult life is approximately proportional to the temperature, and Loeb and Northrop (1916, 1917), working with *Drosophila*, found that the increase is of the same order as that required by van't Hoff's rule for the chemical reactions, *i.e.* that the length of life is nearly doubled by a reduction in the temperature of ten degrees. The figures in support of this conclusion are given in Table XIX.

TABLE XIX.

DURATION OF ADULT LIFE OF *DROSOPHILA* AT DIFFERENT TEMPERATURES.
(After Loeb and Northrop.)

Temperature.	Duration of life in days.	
	Fed on water.	Fed on 1% cane sugar.
34°	2·1	6·2
28	2·4	7·2
24	2·4	9·4
19	4·1	12·3
14	8·3	—
9	11·9	—

The increase, however, is not as regular as in the chemical reactions, since it is relatively greater near the lower limit and smaller near the upper. This type of variation in the temperature coefficient is essentially the same as in that of the rate of development (see p. 22), and in other biological phenomena.

The total duration of life, *i.e.* the period covered by all stages from birth to death, does not vary in accordance with van't Hoff's rule, since the coefficient is greater than two, as required by the rule (Table XX).

TABLE XX.

TOTAL DURATION OF LIFE OF *DROSOPHILA* AT DIFFERENT TEMPERATURES.
(After Loeb and Northrop.)

Temperature.	Duration of life in days.
15°	123·9
20	54·3
25	38·5
30	21·15

Alpatov and Pearl (1929) criticised the methods and the results of Loeb and Northrop. Their conclusion was that the duration of life of *Drosophila* is an exponential function of the temperature and the mean value of Q_{10} in their experiments was 2·07, *i.e.* exactly as required by van't Hoff's rule. They considered, however, that this did not justify the conclusion that the duration of life is determined by a purely chemical reaction and their caution in drawing conclusions from the numerical values of coefficients is perfectly sound.

An interesting result of the experiments by Alpatov and Pearl was the demonstration of a considerable difference between the two sexes of *Drosophila* in longevity, the females always living longer than the males. This is illustrated by Fig. 12.

Janisch (1930, as well as his earlier papers) has recently paid special attention to the problem of the total duration of life as affected by temperature conditions. In the light of his experiments on several insects, and of theoretical considerations, this author derived a curve of the duration of life as affected by temperature (Fig. 13). This curve is an asymmetrical catenary one, and shows, first of all, the characteristic prolongation of life at low temperatures within the vital zone, as observed by many authors. The lowest point of the curve corresponds to the optimum temperature, *i.e.* to the temperature at which the insect develops most rapidly and reaches its physiological death within the shortest time. The optimum, according to Janisch, is a point in the temperature scale, and not a zone, and every departure from this point, however slight, is injurious to the organism. At the temperatures above the optimum point, the velocity of development decreases and the duration of life increases up to the upper critical point beyond which the zone of critical heat begins. Within this zone, the length of life decreases rapidly and the higher the temperature, the earlier in its development the insect dies (Fig. 14), until the point is reached

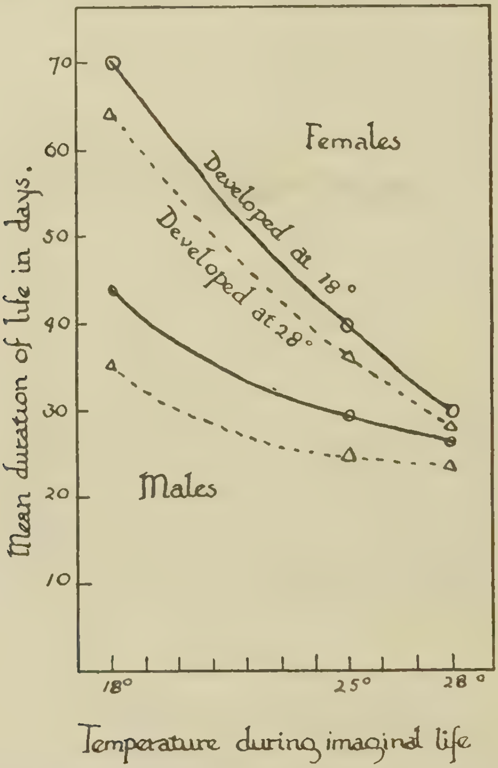

FIG. 12.—The average duration of life of males (two lower curves) and females (upper curves) of *Drosophila* at 18° (black lines) and at 28° (dotted lines). (Re-drawn after Alpatov and Pearl, 1929.)

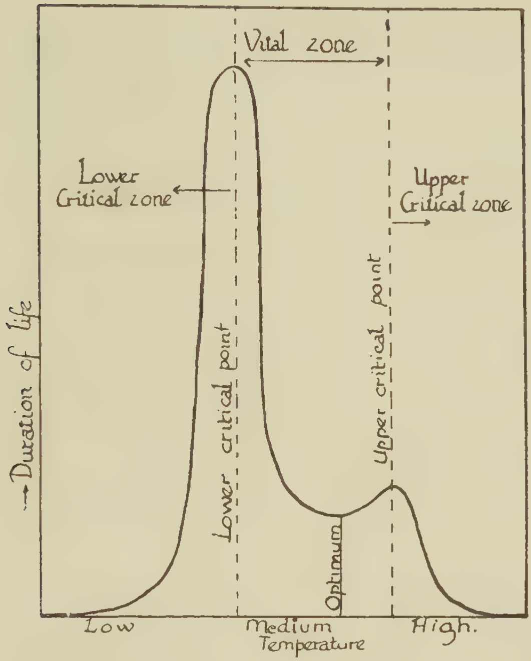

FIG. 13.—Diagrammatic representation of the relation between temperature and the total duration of life of an insect according to Janisch. (Re-drawn after Janisch, 1930.)

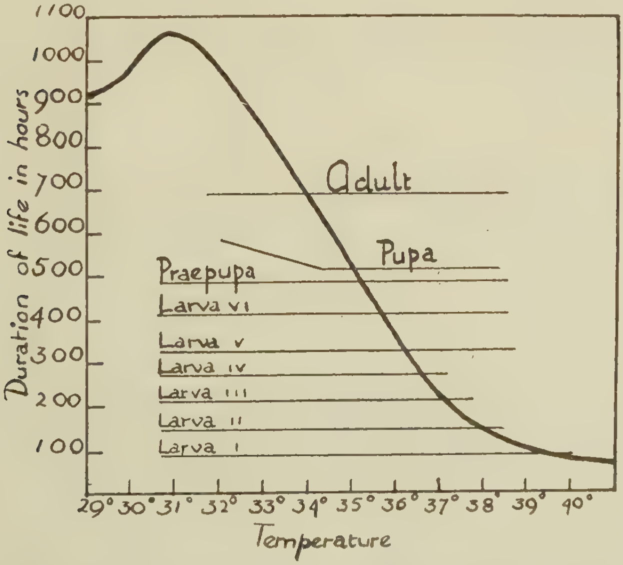

FIG. 14.—The duration of life of *Prodenia* at different high temperatures. The points where the curve crosses the horizontal lines indicate at which stage death occurs at the respective temperature. (Re-drawn after Janisch, 1930.)

when the egg does not develop at all. Even short exposures of eggs to a high temperature have the same effect of shortening the total life.

This theory, while attractive because of its logical appeal, must overcome one serious objection before it is universally accepted, namely, that the figures on which the curve (Fig. 13) is based are not the values observed in the experiments but those calculated by him with the help of his formulae, and the actual experimental data quoted by Janisch are both very insufficient in number and present considerable deviations from the calculated figures for the same points.

Still less convincing are Janisch's considerations on the influence on the duration of life of temperatures below the lower critical point. His curve requires that temperatures below the optimum, but above the lower critical point, should retard the development and increase the duration of life, even if not acting continuously, but during short exposures. This requirement is in obvious contradiction to the experimental data of a number of independent investigators (see p. 33), which have proved definitely the accelerating influence of exposures to low temperatures. Indeed, Janisch's idea as to the invariably injurious effect of any deviations, even temporary ones, from the optimum point (not zone) is based mainly on theoretical considerations, while the data in its support are inadequate and those against it too numerous to be ignored.

That the temperatures well below the optimum may be definitely injurious, the injury manifesting itself not immediately but at later stages in the development, has been shown elsewhere (see p. 36). The data there quoted favour Janisch's theory as far as large deviations from the optimum are concerned, but they do not supply sufficient evidence for all his conclusions. As a temporary working hypothesis, the theory of Janisch may prove useful, since it draws attention to the necessity and importance of fundamental research on the problem of the duration of life as affected by fluctuating temperatures. However, his contention that his exponential curves and formulae represent the final word on the problem, and can be used for practical ecological work, appears somewhat premature.

(*l*) **The Preferendum.**

If an active insect is placed so that a choice of several temperature conditions is possible, it usually moves about for some time and finally rests in a certain temperature zone. This temperature apparently preferred by the insect is called the *preferendum* (the term suggested by C. B. Williams; see Bodenheimer and Schenkin, 1928). The actual preferred temperature varies greatly with different species of insects. Thus, human lice were found by Martini (1917) to congregate within the limits of 24–32°. The larvae of the grasshopper *Camnula pellucida*, Scudd., prefer the temperature 36·6–37·7° (Parker, 1924). House-flies in Lodge's experiments (1918) congregated round the lighted Bunsen burner in a circle with a temperature of 42–44°. Similar unrelated data can be found in other papers, particularly those dealing with thermotropism in insects.

Systematic studies on the problem of preferred temperatures have recently been started by Herter (1923–1925*a*), who has constructed a special apparatus ("Temperaturorgel") for the experiments. This consists of a long glass cage with a metal floor, which is heated at one end of the cage. In this way a gradient of temperature conditions is obtained within the cage and the insects placed in it have a wide choice. The temperature in the cage is measured by several thermometers placed at equal distances from each other. The temperature at any intermediate point can be obtained by interpolation. Herter's experiments have led him to the conclusion that each insect has a definite and somewhat narrow temperature zone within which it comes to rest. The preferred temperature is affected by other factors, such as hunger, sexual activity, light, etc. The temperature of the environment from which the insect has been taken also influences the preferred temperature, as is shown in the following table (Table XXI; Herter, 1923*a*).

TABLE XXI.

PREFERENDUM OF *FORMICA RUFA*, L., AS DEPENDENT ON THE INITIAL TEMPERATURE (After Herter.)

Initial temperature.	Preferendum.
3– 5°	23·29
5– 7	23·63
7– 9	24·71
9–11	24·28
11–13	25·75
13–15	27·88
15–17	28·13
17–19	29·72
19–21	31·26
21–23	31·26
23–25	32·30
25–27	32·22
27–29	32·52

The figures of this table (Table XXI) suggest that the preferendum increases with the initial temperature.

Bodenheimer and Schenkin (1928) have repeated Herter's experiments with several insects, using large numbers of them and taking very numerous readings so as to minimise the chance of observational inaccuracies. As a result, the preferendum proved to be not a strictly defined point, but a fairly wide zone, since 50–80% of the individual insects collect within a zone 4–14 degrees wide. The average figure, however, is useful for obtaining a general idea of the reaction of the insect to various temperatures. The dependence of the preferendum on the initial temperature was found to be very great. For example, the beetle *Tribolium confusum*, Duv., had the preferendum 24·76–26·56° if the initial temperature was 15–18°, but the beetles kept for a month in a thermostat at 25° at first congregated in the zone between 9° and 11°. After several hours, they reverted to the normal preferendum. It is particularly interesting to note that the thermostat beetles behaved in the same way even after being kept for over a month at the room temperature. This indicates that a month at 25° resulted in some deep physiological modification, not entirely obliterated even by an equally long sojourn in a normal temperature.

Bodenheimer's (1930) work on the Desert Locust, *Schistocerca gregaria*, Forsk., is of special value, because it comprised all stages of the insect. The regular increase in the preferendum temperature with the development of the insect is very striking (Table XXII).

TABLE XXII.

PREFERENDUM TEMPERATURES OF THE DESERT LOCUST. (After Bodenheimer.)

Stage.	Preferred temperature.
Egg-laying adults (March)	29·4°
Hoppers of the 1st stage	30·1
,, ,, 2nd ,, ...	28·8
,, ,, 3rd ,, ...	31·6
,, ,, 4th ,, ...	37·1
,, ,, 5th ,, ...	36·7
Young adults (May)	39·3

The difference in the preferendum temperature of the old and the young adults cannot be explained by the higher environmental temperatures in the case of the latter, since experiments with hoppers of the same stage in March and in May did not reveal any difference. The young and the old adults must differ physiologically and this affects their reaction towards the temperature.

Working with ants, Bodenheimer and Klein (1930) again arrived at the conclusion that the preferendum of each species remains practically constant in different months, in spite of the great differences in the environmental temperatures.

The biological value of the preferendum is very great. This is probably one of the most potent factors influencing the ecological distribution of insects and their movements. It appears imperative, therefore, that the preferendum should be determined for each stage of every insect of economic importance. There can be no doubt that its study will go a long way towards helping entomologists to understand the behaviour and distribution of insects.

(*m*) **Limits and Rate of Activity.**

The influence of external temperatures on different activities of insects is discussed in a special section (see p. 87). It is proposed here only to present the main principles of the relation of temperature to the limits and the rate of general activities.

Scattered data bearing on this problem and referring mainly to more or less inexact field observations can be found throughout both the general literature of entomology and that of applied entomology. (The following papers may be quoted as examples: Brunbauer, 1883; Fielde, 1904; Graber, 1887; Grevillius, 1905; Hunter and Pierce, 1922; Kiritchenko, 1926; D. Miller, 1929; Nikolsky, 1925; Parker, 1924, 1929, 1930; Rudolfs, 1922; Strachov-Koltchin, 1915; Sanderson, 1910; Uvarov, 1928; Wille, 1920; Williams and Bishara, 1929). So far, however, practically no experimental investigations have been undertaken, and Bodenheimer (1930) was apparently the first to formulate certain general principles. He suggested that the following phases of general activity in the ascending or descending scale of temperatures should be distinguished:

Phase 1. Beginning of cold stupor.
Phase 2. Very slight movements of antennae and extremities.
Phase 3. The intermittent crawling of the insects.
Phase 4. Normal activity.
Phase 5. Strong activity.
Phase 6. Strong excitement.
Phase 7. Beginning of heat stupor.
Phase 8. Death from heat.

Bodenheimer applied this scale to his studies on the temperature reactions of the Desert Locust, *Schistocerca gregaria*, Forsk. The individual insects in his experiments were placed in a cage, the temperature of which was gradually lowered or raised to the extreme limits. The temperature reactions of each insect experimented upon were classified according to the scale indicated above, and the experiment was repeated with a considerable number of individuals of each stage. A summary of the data is presented in Table XXIII.

TABLE XXIII.

Activity of *Schistocerca gregaria* at Different Temperatures.
(After Bodenheimer.)

Stages.	Phases of activity.							
	1.	2.	3.	4.	5.	6.	7.	8.
	Temperatures at which each phase begins.							
Adult male, March . .	4·9°	10·5°	18·0°	20·1°	32·6°	41·8°	48·4°	50·5°
Adult female, March . .	3·8	7·7	18·5	20·3	30·0	41·5	47·7	50·1
1st larva	4·3	8·2	16·9	21·7	36·2	41·5	—	47·4
2nd larva	6·4	9·8	18·0	25·9	40·0	46·9	51·4	52·3
3rd larva	3·3	4·3	15·3	20·7	37·0	41·9	49·3	50·4
4th larva	4·6	4·6	16·8	26·9	39·2	43·3	49·1	51·4
5th larva	5·5	7·6	20·7	26·0	36·9	45·3	49·2	51·0
Adult male, May . .	4·2	8·0	21·2	25·3	31·5	44·4	51·4	52·3
Adult female, May . .	4·2	7·9	19·9	24·5	31·7	44·3	50·5	52·0
Average . . .	4·6	7·8	18·4	23·5	34·9	43·4	49·6	50·9

The normal activity range comprising phases 4 and 5 of the scale lay between 23·5° and 43·4°, *i.e.* it covered about 20°.

This activity range and the limits of its various phases are very variable in different insects, as was shown in the interesting experiments on the temperature reactions of various sand-dune insects, by Chapman, Mickel, and others (1926). The insects in these experiments were placed in glass tubes, and the temperature was first lowered to 0° and then slowly raised. As the temperature rose, records of activity were made as follows:—Point 1 indicated the first movement of leg or antenna (phase 2 of Bodenheimer), Point 2 represented the stage at which the first individual stood up on its legs, Point 3 when the first crawling was observed (phase 3), Point 4, when all individuals were crawling, Point 5, normal activity (phase 4), Point 6, the first evidence of heat stupor (phase 7), Point 7, when some of the individuals were unable to stand and Point 8, when all individuals were unable to stand. The results of these experiments which are recorded in Fig. 15 are very striking.

In the first place, the figure shows that the insects included in the experiment, although all taken from the same habitat, are not alike in their temperature reactions. This may be explained, in part, by the fact that some of them are nocturnal, and others diurnal, in their habits. Thus, *Geopinus*, which is active at night begins its normal activities (Point 4) at as low a temperature as 7°, while the same point for the wasp *Microbembex* lies at 30°. The range of normal activities (comprising points 4 and 5, and corresponding to the similarly numbered phases of Bodenheimer's scale) varied from 16° in *Melanoplus* to only 2° in *Microbembex*. The extreme narrowness of the range in the latter case is most interesting, as it indicates that even very small fluctuations in the temperature may immediately affect the activities of certain insects.

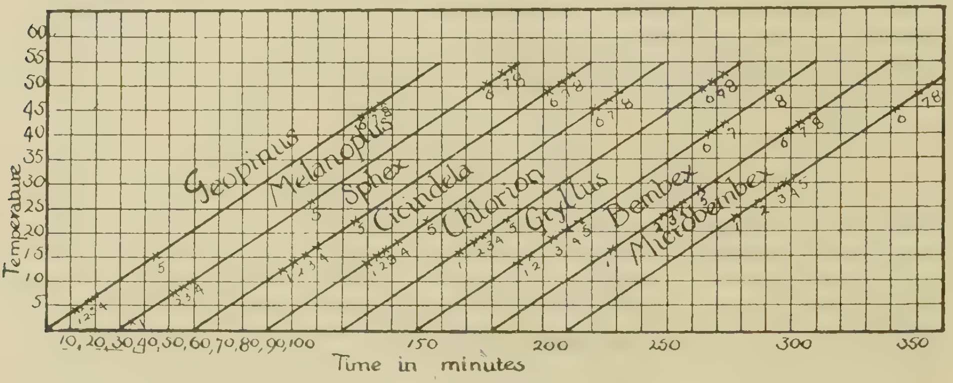

FIG. 15.—Graph showing the results of exposing certain insects from a sand dune to a rising temperature. All insects were inactive at the start. Various degrees of activity are designated by figures, as follows: 1, first movement; 2, first standing; 3, first crawling; 4, all active; 5, normal activity; 6, first paralysis; 7, first insect down; 8, all down. (Re-drawn after Chapman, Mickel, Parker, Miller, and Kelly, 1926.)

The minimum temperature for normal general activity may be still lower than in the case of *Geopinus*. Indeed, in some insects of polar regions, or belonging to winter fauna, it is even below the freezing point (Folsom, 1920; Hormuzaki, 1893; Levander, 1913; Rothke, 1913; Slevogt, 1896; Theuerkauf, 1925). Thus, the winter fly, *Chionea araneoides*, Dalm., has been observed to be active on snow at an air temperature of — 6° (Frey, 1913; see also Boldyrev 1911, 1913; Levander, 1913; Linnaniemi, 1907; Marchand, 1917; Rimsky-

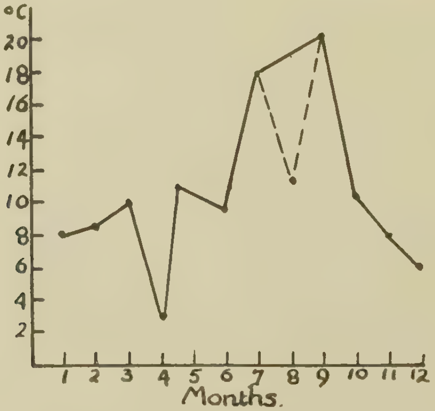

FIG. 16.—Monthly variations in the zero of activity of the ant *Messor semirufus* in Palestine. (Re-drawn after Bodenheimer and Klein, 1930.)

Korsakov, 1925). Arctic bumble-bees visit flowers and are generally fully active at 4° (Friese, 1904). Bodenheimer and Klein (1930) in their studies on the activities of ants in Palestine found that the minimum temperature varied according to the month (Fig. 16). It was 9·2° in January–March, in April 3·5°, in May–June 11·1°, in July–August 18·5°, in September 21·1°, and in October–December 8·4°. This shifting of the zero of activity not in connection with the outer temperature, but with the season, can only be explained by the physiological state of the insects. There appears to be more uniformity with regard to the upper limit of activity.

The rate of activities within the normal limits is not constant, but increases with the rising temperature. This is obvious already from the scales of activity quoted above, while some interesting quantitative data can also be found in the literature. Shapley (1920, 1924; also Shelford, 1929; Szymanski, 1911; Miller and Gans, 1925) studied the speed of running ants at different temperatures and the results conform fairly well to the requirements of van't Hoff's and Arrhenius' formulae (see p. 29). Similar results were obtained, again on ants, by Stumper (1922, 1922*a*) and by Szymanski (1911). Crozier and Stier (1925*a*) came to the conclusion that the rate of abdominal peristaltic locomotor waves in the caterpillars of *Malacosoma americana* is controlled by the temperature according to the Arrhenius' formula. Bodenheimer and Klein (1930), on the contrary, obtained a curve of velocities of running ants at different temperatures which was an equilateral hyperbola. The rate of movement of locust hoppers, *Locusta migratoria*, L., in connection with the temperature has been studied by Nikolsky (1925), who has found that the hoppers of the 5th stage travel 5·22 metres in a minute at 33°, while at 50° their speed increases to 9·8 metres.

In the case of crawling larvae of the fly, *Lucilia sericata*, Meig., there is a slow increase in the rate of locomotion between 10–30°, a rapid drop below 10° and a slow decrease in the rate above 42° (Miller, 1929). Similar results were obtained by Przibram (1909) for the rate of locomotion of Mantids.

A theory of temperature action on the locomotor activities of invertebrates generally has been proposed (Matisse, 1919; Cook, 1928). Two main factors are involved, viz. (1) a chemical factor, *i.e.* the increase in the velocity of reactions with the increasing temperature according to van't Hoff's and Arrhenius' rules; (2) a physical factor, *i.e.* the modification of the granular structure of the colloids of the protoplasm due to heat. Since there are two variables, the temperature and the time (the reaction depending on the length of exposure) the interrelation between them and the rate of locomotion can be expressed only by a three-dimensional curve (see p. 32). Matisse also pointed out that, although both low and high temperatures produce immobility, their action is fundamentally different. Indeed, the torpor produced by a low temperature disappears on the return to a high temperature, but the action of heat is irreversible and produces deep modifications which may be fatal.

Of special interest is the fact that the temperature can affect the reactions of an insect towards other environmental factors, particularly towards light. Responses of the beetle *Taphrocerus gracilis*, Say, to light depend on the temperature. At 30° the beetles are very active and respond positively to light, but at 15° their response to light becomes negative (Chapman, 1923). On the other hand, the flies *Pollenia rudis*, F., are negatively phototropic above 10°, and positively below that point (De Coursey, 1927). Fraenkel (1929) studied the problem with regard to hoppers of the Desert Locust and found that they were positively phototropic when the temperature of the air and of their body was 20°, while at 30–35° they become indifferent to light. This means that a high temperature may inhibit sensibility towards light (see also Grassé, 1922).

The same author observed that geotropism, or reaction to gravity, may also be inhibited by high temperature. The hoppers of the Desert Locust tend to climb up the plants, etc., only at temperatures below 30°, while above it they remain on the ground.

Chapman (1923) found that the reactions of the beetle *Taphrocerus gracilis*, Say, towards mechanical stimuli were inhibited at low temperatures (below 15°), but this may be due merely to the general depression of activities. It is a common experience that almost any insect is more easily disturbed and starts to run or takes to its wings, when the temperature is high.

The above data serve mainly to emphasise how little is known regarding the influence of temperature on insect activities, while the problem is certainly one of the greatest importance. Next to the temperature limits of the development, the limits within which activity is possible must largely determine the degree of adjustment of the species to its habitat, and these limits must be studied in detail for each of the more important economic insects.

The data suggest also that serious experimental studies of the influence of heat on activity must be conducted on the basis of body temperatures and not merely of the temperature of the air. We now therefore turn our attention to the problem of the body temperature of insects.

(*n*) **Body Temperature.**

Reaumur's observation (1740) that the temperature inside a beehive is higher than outside may be considered as apparently the first indication that insects do not depend entirely on the external temperature. He noticed also that the movements of bees' wings serve to raise the temperature within the hive. After him, Hausmann (1803) and Rengger (1817) observed that the temperature in a vial containing live insects was higher than that of the outer air. Newport (1837) made a series of determinations of the external temperature of various insects by pressing a bulb of a small thermometer against the bodies of insects. As the result of his observations he expressed some interesting views, *e.g.* on the connection between body temperature and movement. The first to determine the actual body temperature of insects was Davy (1825), who inserted a very fine thermometer inside the bodies of insects immediately after cutting them open and found that the inner temperature exceeded the outer by 0·5° to 5·8°, although in some cases it was 0·8° to 4·4° lower than the outer temperature. A further advance in the methods of studying the inner temperature of insects was made by Nobili and Melloni (1831), who introduced the thermoelectric method, while Dutrochet (1846) applied it for observations on a fairly large scale. On the basis of his results he criticised the data obtained by Newport (1837). Other authors of the same period included Berthold (1835), Becquerel (1844), Schulz (1877), Breyer (1860) and Dönhoff (1860). The last-named author measured the body temperature of the honey-bee and found that it was higher than the temperature of the air, but that the difference tended to decrease at higher air temperatures. There are in the literature numerous data on the temperature in beehives and its regulation by bees, but it will be more convenient to review them elsewhere (see p. 134).

The first critical survey of the literature on the subject, supplemented by a long series of his own investigations, is that of Girard (1869). The main conclusions reached by him were as follows :—

1. Adult insects never, even in an inactive state, possess a body temperature below that of the surrounding air.
2. Larvae of hemimetabolous insects possess a temperature equal to, or somewhat higher than, the air temperature. In the larvae of holometabolous insects this is not always the case, *e.g.* caterpillars with a smooth skin often possess a temperature below that of the air.
3. The temperature of Hymenoptera is always higher than that of the air, but lower than in Lepidoptera and in Diptera.

Bachmetjew's work (1899, 1901) on the body temperature of insects was of particular interest because he studied it in a more systematic manner than previous authors, varying the external conditions of the experiments. The hawk moth, *Celerio euphorbiae*, L., showed the following changes in the body temperature connected with the gradual rise of the external temperature (Table XXIV).

TABLE XXIV.

Body Temperature of Adult *Celerio euphorbiae*. (After Bachmetjew.)

Air temperature	Body temperature	Difference.	Air temperature	Body temperature	Difference.
37·0°	36·7°	—0·3°	47·6°	45·1°	—2·5°
38·4	37·7	—0·7	49·0	47·0	—2·0
39·2	38·4	—0·8	49·8	48·1	—1·7
40·0	38·7	—1·3	50·0	48·6	—1·4
41·5	39·8	—1·7	50·4	49·7	—0·7
45·4	44·1	—1·3	51·2	51·0	—0·2
46·1	44·5	—1·6	51·5	51·4	—0·1
47·0	44·8	—2·2			

This table (Table XXIV) shows that the temperature of the moth lags more and more behind the air temperature with the rise of the latter, beginning to approach it again near the upper limit of activity. At the fatal point the body temperature and the air temperature become equal.

Bachmetjew's observations on the body temperature were made mainly under extreme conditions, with a view to determining the two fatal points, and they do not explain the influence of external temperature on that of the body within the normal, *i.e.* the medium, range of temperatures.

Brünnich (1919) was the next author to study the body temperature of insects, and he used bees for his experiments. He found that the body temperature of active working bees may reach 39·6°, while that of drones may be even as high as 48·4°. There was, however, a very considerable individual variation under the same conditions, and Pirsch (1923) ascribed this lack of uniformity in Brünnich's results to certain faults in the technique of the thermocouple method. Pirsch himself also worked on the honey-bee, and made very numerous determinations of the body temperature of individual bees at different air temperatures. The results of his determinations are shown in the following table (Table XXV) and in Fig. 17.

The average body temperature of a bee is, thus, considerably higher than that of the air when the latter is low (*e.g.* 5·5°). As the air temperature increases, the difference between it and the body temperature of the bee decreases, until at 35° the two approach each other very closely. In the interval between 35·0° and 43·5° the two temperatures run together, while a considerable negative difference becomes obvious near the upper fatal limit. Wing movements cause the body temperature to rise considerably, so that a bee cannot be regarded as wholly dependent on the temperature of its environment. (See also W. Park, 1923*a*; Schulz, 1877; Bruman and Liechti, 1929.)

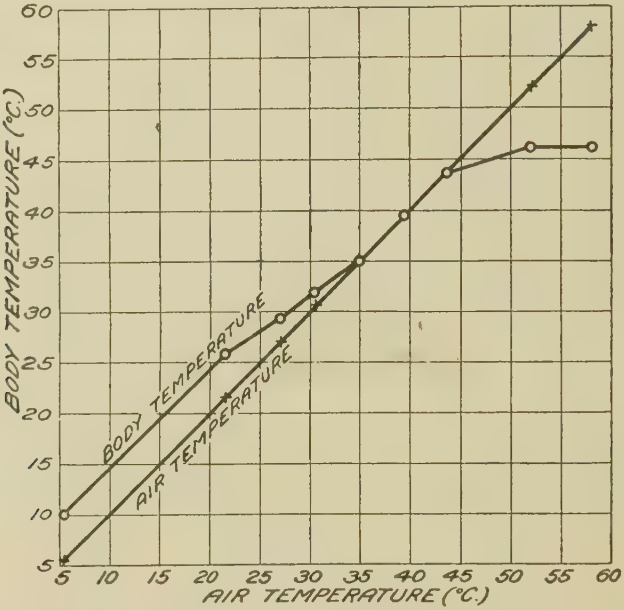

FIG. 17.—Relation of body temperature of the honey-bee to the air temperature. (After Pirsch, 1923.)

TABLE XXV.

BODY TEMPERATURE OF THE HONEY-BEE. (After Pirsch).

Air temperature.	Body temperature.			Difference between air temperature and average body temperature.
	Maximum.	Minimum.	Average.	
5·5°	14°	8·5°	10·2°	4·7°
21·4	31	22	25·8	4·4
27·0	30	28·5	29·1	2·1
30·5	34	31·5	32·0	1·5
35·0	37	34·5	35·1	0·1
39·5	42	38·0	39·5	0·0
43·5	44	42·5	43·6	0·1
52·0	48	45·5	46·0	— 6·0
58·0	48	45·5	46·4	—11·6

More recently Himmer (1925) determined the average excess of the body temperature above that of the air as 12·4° in the case of the honey-bee, 10·48° in *Vespa vulgaris*, L., and 3·08° in *Polistes gallica*, L. The figures apply apparently to active insects.

(i) *Factors affecting Body Temperature.*

Newport (1837), Dutrochet (1840), Becquerel (1860), Breyer (1860) and Lecoq (1862) discovered that the body temperature of insects depends to a great extent on the *movements* of the insects, which cause the temperature to rise. The problem has been studied in detail by Bachmetjew (1899, 1901), who used in his experiments moths pinned through the sternum on a thermo-electric needle. His determinations of the body temperature of *Saturnia pyri*, L., showed that the temperature was about 18·5–19·9° when the moth was quiet, and rose to 24–24·9° when it fluttered its wings. Brünnich (1919) found that the body temperature of worker bees may rise to 39·6° as a result of the movements of the bees, and that the temperature of drones may be even as high as 48·4°. Dotterweich (1928) studied the body temperature of hawk-moths, also by the thermo-electric method, but the point piercing the insect's body was attached to a long thread, so that the insect could actually fly in its cage. His data revealed the interesting fact that the fluttering of the wings (" humming ") preliminary to flight serves to raise the body temperature to a certain point, below which flight does not occur. In one of his experiments the body temperature rose from 9° in the resting insect to 22°, after some " humming." When it reached 34° the moth began to fly and its temperature rose to 41·5°. The moth " hummed " longer when the external temperature was lower, and always began to fly when the body temperature reached approximately the same point.

It is, however, not quite clear whether such movements are able to increase considerably the temperature of the whole body. Indeed, all exact determinations were made by means of a thermo-electric needle inserted into the thorax, *i.e.* into, or close to, the thoracic muscles which are concerned in the wing movements. A rise of the temperature in the thorax does not mean that the temperature of the whole body rises to the same extent. Dutrochet (1840) has found, in fact, that the temperature in the abdomen is somewhat lower than that in the thorax, but his are the only experiments bearing on this problem.

A factor greatly affecting body temperature is the *humidity of the air*. Observations on this problem have been made by Dutrochet (1840) and Girard (1869), as well as by Bachmetjew (1901). The last-named author reached the conclusion that the body temperature of insects is lower than that of the air, if the latter is of normal humidity, while in very damp air the body temperature is higher than that of the air. Two factors are responsible for this, viz. the evaporation of water from the body, which lowers the body temperature, and the respiration, which increases it. The actual body temperature is, therefore, the resultant of the relative effectiveness of these factors.

The importance of evaporation, and of all factors influencing its rate, for the body temperature of insects has been urged by Shelford (1914) but mainly on theoretical grounds, without the necessary experimental data. Necheles (1924) supplied such data with regard to *Blatta orientalis*, L. He found that between 13° and 23° the body temperature of the cockroach runs parallel to the air temperature, while above 23°, in dry air, the body temperature lags behind that of the air. In moist air it increases more rapidly than the air temperature. This difference must be due to increased evaporation in the dry air.

Buxton (1924) compared the body temperature of a living and a dead black Tenebrionid beetle (*Adesmia*) exposed to the sun, and found that a dead insect was by 2–9° hotter than a living one (Fig. 18). This suggests that the body temperature of a living insect is probably regulated by the loss of water through respiration.

Some recent work has shown that in studies on the body temperature of insects special attention should be paid to *radiation*, a factor which has been much neglected in the past. Franz (1930) proved that the body temperature of the grasshopper *Oedipoda coerulescens*, L., rises steeply shortly after sunrise and falls again after sunset, while during the day it follows rather closely the temperature of the layer of the air nearest the ground. This temperature is very different from that of the upper layers, owing to the radiation of the heat by the surface of the ground.

It is well known that the majority of insects are most active during hot, fine weather, their activity obviously depending on the influence of the direct sun-rays, but no attempt has been made to correlate activity with the body temperature as influenced by the radiant heat. In 1928 I pointed out the need for the study of this factor for a better understanding of the activities (movements generally and migrations in particular) of locust hoppers, and interesting recent observations by Bodenheimer (1930) have emphasised the soundness of this view. The body temperature of hoppers of the Desert Locust, *Schistocerca gregaria*, Forsk., was found by him to rise rapidly in the morning to over 40°, while during the daytime it fluctuated between 40° and 45°. While this temperature is considerably below that of the black-bulb and the white-bulb thermometer in vacuo, it is well above the air temperature in the sun, recorded by an ordinary thermometer, and above that on the surface of the soil. Table XXVI and Fig. 19 illustrate this observation very clearly.

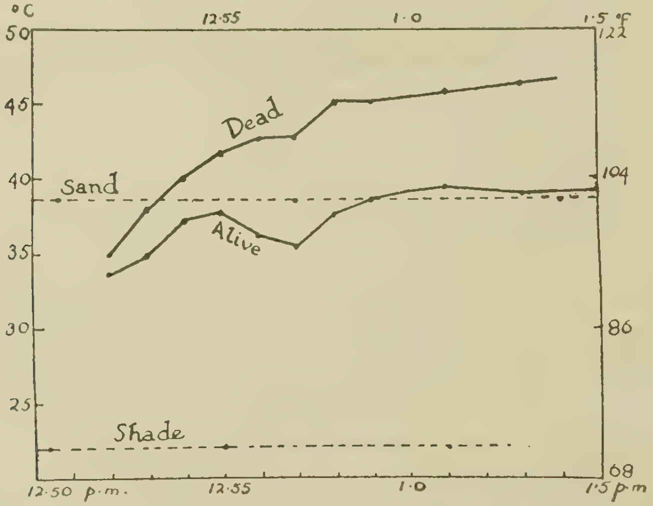

Fig. 18.—The body temperature of a living and a dead black beetle (*Adesmia*) exposed to the direct sunlight on sand. (Re-drawn after Buxton, 1924.)

When comparing the curve of the body temperature with this table (Table XXVI), one is struck by the sharp falls in the temperature at 6 a.m., 8.10 a.m. and 8.50 a.m., corresponding exactly to the periods when the sun was temporarily obscured. The absorption of heat by the bodies of hoppers must be very intensive and must have a very quick response, while the inability of the insects to maintain their body temperature in the absence of direct sunlight

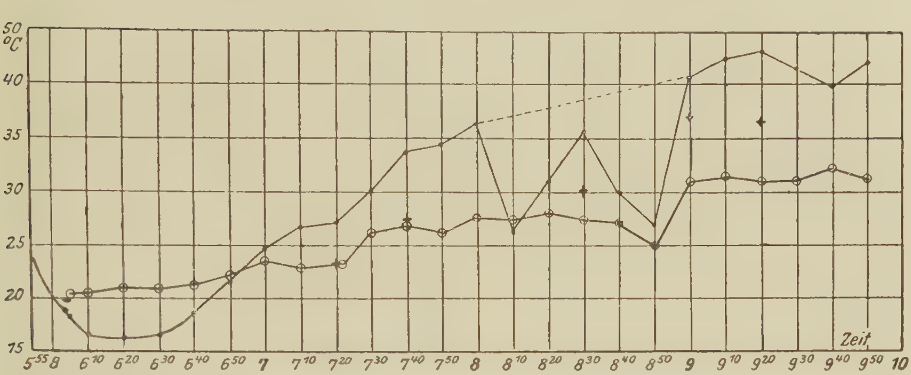

Fig. 19.—The upper curve represents the body temperature of hoppers of the Desert Locust in the morning; the lower curve is that of the air temperature in the sun; crosses, the temperature on the surface of the ground. (After Bodenheimer, 1930.)

TABLE XXVI.

Body Temperature of Hoppers of the Desert Locust. (After Bodenheimer, 1930.)

Time, a.m.	Body temperature.	Vacuum thermometer readings.		Air temperature.		Temperature on the soil surface.	Sun.	Wind.
		Black bulb.	White bulb.	In the sun.	In the shade.			
5.55	23·5°	20·8	20·7	—	—	—	Shade	No wind
6.05	18·5	20·4	18·7	20·4°	19·8°	—	,,	,,
6.10	16·5	20·4	18·5	20·4	19·8	—	,,	,,
6.20	16·3	20·2	18·5	20·9	19·0	—	,,	,,
6.30	16·5	20·3	18·6	20·9	18·9	—	,,	,,
6.40	18·5	23·2	20·1	21·3	19·9	—	Sun	,,
6.50	21·5	31·1	22·3	22·3	20·5	—	,,	,,
7.00	24·5	38·0	26·8	23·5	20·9	—	,,	,,
7.10	26·5	42·1	30·7	22·9	21·3	—	Bright sun	,,
7.20	27·0	44·8	33·1	23·0	21·2	23·0°	,,	,,
7.30	30·0	45·0	34·7	26·0	21·3	—	,,	,,
7.40	33·6	51·1	37·6	26·7	22·2	27·3	,,	,,
7.50	34·3	52·3	38·4	26·5	22·0	—	,,	Slight breeze
8.00	36·2	57·9	39·7	27·5	23·9	—	,,	,,
8.10	26·2	40·0	37·0	27·4	23·0	—	Shade	,,
8.20	30·7	50·1	40·3	28·0	23·0	—	Sun	,,
8.30	35·4	59·0	41·0	27·3	24·0	30·0	,,	,,
8.40	29·9	47·0	35·5	26·0	24·0	—	Slight shade	,,
8.50	27·0	41·0	31·0	25·0	24·0	—	,,	,,
9.00	41·8	63·5	45·0	31·0	25·0	37·0	Sun	,,
9.10	42·3	65·2	46·0	31·5	25·5	—	,,	,,
9.20	42·8	66·0	46·7	31·0	25·9	36·5	,,	,,
9.30	41·4	65·0	46·5	31·0	26·0	—	,,	Stronger wind
9.40	39·9	65·6	47·5	32·2	25·0	—	,,	Slighter wind
9.50	42·0	65·5	48·6	31·3	26·2	—	,,	Stronger wind

is also quite obvious. There is hardly any doubt that this intimate connection between the body temperature of locust hoppers and the radiant heat depends on their coloration, which is mainly black and which must favour the absorption of the infra-red heat rays.

These observations show the importance of the coloration of insects in their thermal economy. This problem has been much neglected by the numerous students of insect coloration, who have regarded the latter as a character of certain evolutionary value, but not as a physiological factor of great importance. There have, however, been some exceptions. Lord Walsingham (1885), nearly half a century ago, put forward certain suggestions on the subject of melanistic coloration in Lepidoptera, which is of very common occurrence in arctic countries. He suggested that their dark coloration is important from the point of view of absorption of the heat of the sun-rays. A dark coloured insect may utilise even short intervals of sunny weather for its activities, while a white one would be still inactive. He made an experiment of placing on the surface of snow some Lepidoptera of different colour, viz. the black *Odezia atrata*, L., and the white *Acidalia immutata*, L. The temperature in the sun was 8·88°, and even after half an hour marked signs of melting of the snow under *Odezia* were observed, while none were noticed under the white moth. Several other writers have also drawn attention to the prevalence of black coloration in insects occurring in cold climates. Handschin, in particular (1919, 1919*a*, 1925), pointed out that many of the insects occurring in the nival zone of the Alps are dark coloured. This applies specially to Collembola, living on the snow, which are always black (see also R. Parker, 1921; Vorbrodt, 1922).

An attempt to formulate a theory of coloration based on the principle of absorption of radiant heat was made by Schröder (1903). His observations on the caterpillars of several species of moths demonstrated that a low temperature increased the amount of dark pigment in their skin, and he suggested that by this means the caterpillars partly paralyse the inhibiting effect of low temperatures by increasing the absorption of heat. He made also some determinations of the absorption of heat by normal Lepidoptera and the respective melanistic aberrations, with the not unexpected result that the black scales of the aberrations were found to possess a greater absorptive power than the white scales of the typical forms. Unfortunately, the actual records of Schröder's experiments have never been published. Later, in 1927 he extended his theory to insects with sympathetic coloration, *i.e.* insects coloured according to the colour of their environment. He suggested that the sympathetic pigments are best suited to absorb the heat radiated by the surrounding objects. This suggestion may be worth checking. Schröder himself remained on purely theoretical ground and did not publish any facts to support his suggestions. Prochnow (1926–27, 1927) criticised Schröder's theories very severely, but also without any serious evidence of fact.

Szilady (1921), apparently independently of Walsingham and Schröder, emphasised the importance of colour, particularly of the black pigmentation, in the absorption of heat, but again this was made on purely theoretical grounds.

The same author, as well as Lengerken (1924–27), suggested that the metallic colours of beetles living in full sunshine may serve for the purpose of reflecting heat rays.

Krüger (1929) studied the reflection of infra-red rays by the surface of some butterflies and found that, for example, the body integuments of *Parnassius* *apollo*, L., absorb the infra-red rays almost wholly, while the wings reflect a considerable percentage of them.

The conception of the possible rôle of coloration in the thermal economy of insects has thus been expressed repeatedly, but there are practically no data in support of it. Indeed, apart from the data on locust hoppers obtained by Bodenheimer, very few attempts have been made to study the problem experimentally. Interesting observations were made by Buxton (1924*a*) on the body temperature of the grasshopper *Kripa coelesyriensis*, G. T., which occurs in two colour forms, one buff, another blackish-brown. When individuals of both forms were exposed to the sun, the dark form became 4–5° hotter than the buff.

There is no doubt that many insects are able to regulate their body temperature as affected by radiant heat, by certain movements. This has been observed by Fraenkel (1929, 1930; also Bodenheimer, 1930) in the hoppers of the Desert Locust, *Schistocerca gregaria*, Forsk., which place their body either parallel, or perpendicular, to the sun's rays, according to the intensity of the heat. Thus, in the morning the hoppers place their bodies so that their sides are exposed to the rays, while, when it becomes hot, they sit facing the sun, thus reducing the absorbing surface. Determinations of the body temperature showed that the average figure for the hoppers sitting with their bodies perpendicular to the sun's rays was 41·7°, while for those with their bodies parallel to the rays, it only reached 38·3°. The difference fluctuated between 2° and 4°. There is little doubt that similar behaviour reactions towards radiant heat, serving to regulate the body temperature, will be observed in other insects. Moreover, one may expect to find a clue to the understanding of certain movements and resting attitudes of insects in the study of their correlation with radiant heat and with the body temperature.

(ii) *General Conclusions.*

I have paid special attention to the collection of the data on the body temperature of insects and the factors influencing it, but the results, as presented above, must be considered far from satisfactory. Indeed, the information available is most fragmentary, and there is a practically virgin field for further investigations.

There is scarcely any need to stress the importance of such investigations. I would like, however, specially to point out that the influence of the external temperature on the activities of insects is not direct, but acts through their body temperature. This view has already been expressed, with regard to the behaviour of locust hoppers, by myself (Uvarov, 1928) and the observations by Bodenheimer (1930) tend to support it. In other sections (p. 87) data are collected on the influence of temperature on the various activities of insects. It stands to reason that all these data are only of a relative character, since they refer to the external temperatures, and activities must be governed by them not directly, but through the body temperature which has never been studied in this connection.

Further, all our knowledge of the interrelations between the development of insects and temperature conditions is also based on the erroneous assumption that the external temperature affects the rate of development directly, and none of the formulae and curves introduced to illustrate the relation take into consideration the important complications connected with the absorption and utilisation of heat by the insect. I do not mean that we shall be unable to understand fully the relation between development and temperature until we have studied the thermodynamics of the insect body in all its details. I think, however, that sufficient evidence has been accumulated to make it impossible to regard insects as absolutely dependent on the external temperatures. The study of body temperatures, as affected by external conditions, will, no doubt, explain many difficult points in the problem of the relation of development to temperature. The technique of such work is bound to be very difficult, but the difficulties should not be an excuse for adopting easier, though obviously less reliable, methods.

These latter can properly be applied when only approximate results are needed, but authors who aim at expressing the relation between temperature and development by very exact formulae and curves should base their mathematical speculations on more reliable data than the external temperatures, which often differ considerably from the body temperatures, the difference, moreover, not being constant.

II. HUMIDITY.

(*a*) Vital Limits.

No living organism can exist without water, since the latter constitutes the major part of living tissue, and all the vital processes within the organism require water for their accomplishment.

The water necessary for the insect organism is in most cases obtained with food, and the water content of the food is of great importance. In the case of insects feeding on succulent tissues of plants the problem of obtaining sufficient water is not difficult, but the quantity of water available often depends on climatic factors, *i.e.* on the precipitation and evaporation, which determine the water content of the plant. This indirect influence of climatic factors upon insects is discussed elsewhere (see p. 150).

In the case of insects living upon very dry food, *e.g.* on dead wood, or seeds, the amount of water obtained with the food is very small, and such insects undoubtedly have to rely mainly on the water resulting from metabolic processes. This can also be said with regard to insects living in deserts. The latter may, however, have other sources of water which are not yet sufficiently known, as has been shown by Buxton (1924*a*), who has pointed out that dry fragments of vegetation, which are common in the driest deserts, absorb moisture from the air at night, and retain it until after sunrise. These fragments are eaten by some phytophagous insects, and supply them with water. Breitenbrecher's (1918) observations proved that insects can absorb water directly from the air, and increase in weight. The absorption was greater at higher temperatures, and practically ceased below 12°.

Robinson (1928*a*) made an interesting series of estimations of the water content of various insects, and of their food (see Table XXVII).

The dependence of the water balance in insects upon the water content of their food is demonstrated very clearly by this table (Table XXVII), and we see that insects living on dry food, *e.g.* weevils and the locust borer, have a low water content, while the water content of the leaf-eating species is very high.

In the case of insects with low water content the problem of the conservation of the water in their organism must be of the greatest importance, more especially since the surface area of a small creature, such as an insect, is very

TABLE XXVII.

WATER CONTENT OF INSECTS AND OF THEIR FOOD. (After Robinson.)

Species.	Food plant.	Water content of food, %.	Water content of insects, %.
Granary Weevil, adult (*Sitophilus granarius*) . .	Stored wheat	9–11	46–47
Rice Weevil, adult (*Sitophilus oryzae*)	Stored wheat	15–16	48–50
Locust Borer, adult (*Cyllene robiniae*)	Locust tree trunk	30–32	56–60
Colorado Potato Beetle, adult (*Leptinotarsa decemlineata*) .	Potato plant, leaves and stem	70–74	62–66
White grub, larva (*Phyllophaga* spp.) . . .	Wheat shoots and roots	64–67	73–82
Mourning Cloak, larva (*Vanessa antiopa*)	Willow leaves	70–73	77–79
Willow Sawfly, larva (*Cimbex americana*) . . .	Willow leaves	70–73	79–82
Cutworm, larva (*Chorizagrotis auxiliaris*) . . .	Lettuce	78–79	83–88
Army Worm, larva (*Cirphis unipuncta*) . . .	Corn leaves and stem	77–78	87–89
Imported Cabbage Worm (*Pieris rapae*) . . .	Cabbage	88–89	83–84
Polyphemus Moth, larva (*Telea polyphemus*) . .	Hazel leaves	71–73	90–92

great compared with its volume, the ratio being much more unfavourable than in the case of larger animals (Kennedy, 1927). Unfortunately, scarcely anything is known regarding the factors affecting the water balance of living insects, and investigations on this problem are greatly to be desired. In such investigations it would be necessary to pay attention not only to the total water content of the insect, but also to the form in which the water is present. Robinson (1928*a*) has pointed out that it may be present either as free water, which is naturally easily lost, and also as water bound by colloids, which remains practically unaffected by the external conditions. Robinson's studies have proved that in those species which live on relatively dry food and have a low water content a large percentage of the total water is bound by colloids. For example, the granary weevil, which has only 46% of total water, has 50% of it in a bound condition. The rice weevil, with slightly more total water, namely 48%, has a smaller proportion of it, viz. 35% bound. The locust borer, with 58% total water, has 29% of it bound. On the other hand, the species living on moist food and having a high water content, ranging from 58 to 92%, have only 3–9% of it bound. This must affect the resistance of the respective species against desiccation in a most fundamental way, and an extensive study of the water relations of insects of various habits and habitats should throw much light on the various problems of their ecology and bionomics. (For a discussion of the water content of insects in connection with their cold resistance, see p. 12.)

The fatal limit of desiccation cannot be the same in different insects, but so far very little work has been done on this subject. Bachmetjew (1907) observed that the pupae of *Sphinx ligustri*, L., may lose, without dying, up to 80% of their weight during hibernation, obviously through evaporation. Berger (1907) kept larvae of *Tenebrio* in a very dry medium, and they did not lose in their relative water content though they lost in their weight. This indicates that they replaced the water lost through evaporation by the metabolic water. F. Hall (1922) found that the same larvae can be desiccated to 52·6% of their body weight, and survive under these conditions for 1084 hours. Buxton (1930) has shown that a larva of *Tenebrio* can maintain an almost constant proportion of water in its body, during a month's fast, at humidities from 0 to 60%. This is probably done at the expense of the metabolic water. Eggs of grasshoppers may be dried so that they lose up to 51% of their original weight without losing their vitality (Parker, 1929, 1930). Some comparative studies were carried out by Breitenbrecher (1918), in whose experiments the potato beetle, *Leptinotarsa decemlineata*, Say, survived a desiccation to less than 50% of its original weight, while the beetle *Cotalpa lanigera*, L., died after losing water to the extent of 25% of the body weight, and the June beetle, *Lachnosterna*, did not survive a loss of 15% of its original weight.

The rate of loss of water from the tissues must be connected with the relative humidity of the air as well as with the temperature (see p. 83), but exact data on the favourable and fatal air humidities are very scanty. Gill (1921, 1921*a*) recorded that a mean relative humidity of not less than 48% at 27° is essential for the existence of the mosquito *Culex fatigans*, Wied., while lower humidities are fatal. Headlee (1917*a*, 1918, 1921, 1921*a*) has done a considerable amount of work on this subject, but mainly with regard to the rate of metabolism, as affected by humidity (see p. 72). The lower fatal limit of humidity for the bean weevil, *Bruchus obtectus*, Say, was found by this author at 1% relative humidity, at which no individuals succeeded in reaching maturity. At 7·1% very few of the insects developed. The percentage of mortality was lower at 25·9% relative humidity, while the optimum proved to lie between 80% and 89%. The optimum percentage of humidity was actually the highest below that which encourages the growth of fungi. In other words, even higher humidities might have been favourable to the insect, were they not favourable to the fungi. In the case of Collembola (Davies, 1928), the requirements for the air humidity are very high, and a saturated atmosphere is necessary for their survival. In a dry atmosphere (0% relative humidity) *Isotoma viridis*, Bourl., and *Tomocerus vulgaris*, Tullb., succumb within 20 minutes, and even at 50% humidity they do not survive for more than an hour. The pupae of *Drosophila* are also highly susceptible to dryness (Elwyn, 1917), the percentage of mortality increasing with the decrease in humidity (see Table XXVIII).

TABLE XXVIII.

MORTALITY OF *DROSOPHILA* PUPAE, AS AFFECTED BY RELATIVE HUMIDITY.
(After Elwyn.)

Relative humidity . . .	100	61·66	0
Mortality per cent. . . .	2·5	12·3	52·9

Janisch (1930) studied the influence of relative humidity on *Prodenia litura*, F. At 0% humidity only about 30% of the eggs hatched, while at 70% humidity the caterpillars that developed died within the egg-shells.

Peterson (1917, 1920) has supplied some data on Aphids, the eggs of which give the highest percentage of hatching at 80-100% humidity.

According to Bodenheimer's (1930) observations, the earlier stages in the embryonic development of eggs of the Desert Locust, *Schistocerca gregaria*, Forsk., are more susceptible to the humidity factor than the later stages. Thus, only one-seventh of the number of newly-laid eggs which hatched at 100% humidity, hatched when the eggs were kept at 80% humidity. In the case of eggs which were two-thirds developed, 80% humidity caused the hatching of about a half of the number which would hatch at 100%. The same author also studied the loss of weight and the length of life of starving individuals of the locust at different relative humidities. The results are presented in Table XXIX, from which the favourable influence of higher humidities is apparent.

TABLE XXIX.

Duration of Life of Starving Individuals of the Desert Locust at Different Relative Humidities of the Air. (After Bodenheimer.)

Relative humidity, %.	Duration of life in days.				Average.
	2nd larva.	3rd larva.	5th larva.	Old adults.	
0	4·4	4·1	1·0	2·0	2·9
20	1·0	2·7	1·8	3·0	2·1
40	3·0	5·3	1·5	3·0	3·2
60	3·4	5·5	3·0	4·8	3·9
80	1·5	6·1	2·5	3·0	3·4
100	3·5	4·7	3·0	5·8	4·5

The pupa of *Protoparce quinquemaculatus*, Haw., which is not at all affected by 0% relative humidity (Helfey, 1928), may be quoted as an example of an insect very resistant to dryness.

These examples do not permit the formulation of any general theories concerning the vital limits of relative air humidity. Moreover, they do not even suggest that such limits exist in both directions from the optimum, as no definite cases of direct injurious influence exerted by high air humidity are known, and further researches in the problem are greatly needed.

Another problem in the relation of insects to the humidity of their environment is presented by the insects that live in the soil. We shall show later (see p. 147) how the moisture conditions of the soil determine the distribution of such insects. At this point is mentioned only some experimental work on the subject of the vital limits of soil moisture. It appears that no work has been done on the fatally low soil moisture. As regards the fatally high moisture, this condition would occur when the soil is saturated with water, and the survival of an insect would then depend on its ability to survive submergence in water. Again, scarcely any exact investigations have been undertaken on this problem. There exist only some general observations, *e.g.* those published by the United States Entomological Commission (1878), to the effect that a submergence even for several weeks does not injure the eggs of grasshoppers; or the observations by Predtechenskiĭ (1928*a*) that eggs of the Migratory Locust, *Locusta migratoria*, L., can withstand submergence if the embryos are not yet developed, while eggs submerged in the later stages of the embryonic development show a high percentage of mortality (see also Crowell, 1927). Submergence in flooded, or irrigated, areas is a factor of great importance, and the problem deserves to be studied experimentally.

(*b*) **Development.**

The existing data on the influence of humidity on the rate of development are both scanty and contradictory.

Bachmetjew (1907) and Elwyn (1917) concluded that air humidity has no influence on the velocity of development of the pupae of Lepidoptera and of *Drosophila*, while Urech (1890) found that dry air shortens the pupal period of butterflies. Glenn (1922) studied this problem in some detail with the eggs and pupae of the codling moth, and found that the variation in the length of the embryonic and pupal development was not affected by the relative humidity of the air in any appreciable degree. A similar conclusion was reached with regard to the Aphid, *Toxoptera graminum*, Rond., by Headlee (1914), who found that the air humidity does not affect the rate of metabolism in the insects which feed on succulent food. In the European corn-borer, *Pyrausta nubilalis*, Hb., air humidity has a decided influence on the pupal stage. Deficient humidity raises the threshold of development and decreases the rate of metabolism (Caffrey and Worthley, 1927). Opposite results were obtained by Hennings (1907, 1907*a*) for all stages of *Tomicus typographus*, L., which were delayed in their development by higher humidity. Acqua (1929) found that the rate of development of silkworm-eggs increased with the humidity. (See also Garau, 1872.)

Headlee (1917, 1921, 1921*a*), working with the angoumois grain moth, *Sitotroga cerealella*, Ol., and with the bean weevil, *Bruchus obtectus*, Say, obtained figures indicating that the relation of the metabolic rate to the air humidity is not constant. In the pupae and eggs of both insects the velocity of development varied inversely with the relative humidity of the air. In the adult weevil it varied directly with humidity, in the adult moth inversely as the humidity, and in the larvae of both species it varied with the humidity. In Headlee's opinion, these variations in the response in the rate of metabolism to air humidity support Bachmetjew's (1907) suggestion that for each species there is an optimum humidity, this optimum varying for each species and for each stage. The optimum air humidity depends apparently on the concentration of body fluids, there being an optimum concentration for a given metabolic process. If the water content is well above the optimum, dry air will accelerate the development by removing the superfluous free water, and moist air will retard the development. If the water content is near the optimum, dry air will reduce it, and thus retard the development, while moist air will preserve the optimum conditions, and thus speed up metabolism. Headlee's theory appears very reasonable, and one would like to see it checked by actual studies of the relation of relative humidity of the air, not only to the total water content of insects, but also to the ratio of free and bound water, which must be the deciding factor in the optimum conditions of the body fluids for each of the metabolic processes.

The conception of an optimum air humidity is supported by Janisch's (1930) experiments on the eggs of *Prodenia litura*, F., which developed most rapidly at 90–95% humidity. 100% humidity was equally favourable for the rate of metabolism, but it was often injurious at higher temperatures.

The influence of air humidity on the course taken by development is practically unstudied. Nagamori (1927) studied experimentally the effects of humidity on the number of moults in the silkworm, and found that in dry air all the caterpillars moulted five times, while in humid air a high percentage moulted four times. If the caterpillars of *Pieris brassicae*, L., from which parasitic larvae of *Microgaster glomeratus*, L., are emerging, are placed on wet linen, the larvae do not spin cocoons as they normally would (Dewitz, 1912*a*). In the experiments of Quajat (1903) with silkworms, on the contrary, the amount of silk produced increased if they were kept in a humid atmosphere. In many other insects the transformation from one stage to another is apparently favoured by a certain humidity of the environment (air, or soil, as the case may be). The hatching of eggs of ACRIDIDAE, for example, is often favoured by rain, and the same has been observed with regard to the emergence from their pupae of adults of various insects. In the experiments made by Severin and Severin (1910) on the stick-insect *Diapheromera femorata*, Say, 94% of the individuals hatched in a dry atmosphere failed to extricate themselves completely from the egg-shell. (See also Rau, 1926.)

Some facts are known with regard to the development of coloration and colour pattern. These refer mainly to local and seasonal forms of Lepidoptera. Data on the wet-season and dry-season forms of tropical butterflies are discussed elsewhere (see p. 113), while observations on local forms due apparently to a humid climate are very unconvincing. Thus, G. Hudson (1913) mentions that melanistic forms of Lepidoptera are common in certain parts of New Zealand where the climate is particularly humid. Pictet (1904*a*, 1905*a*) produced experimentally melanistic aberrations in Lepidoptera by feeding the caterpillars on moist food, while Kosminsky (1909) found that humidity has little influence either on pattern and coloration, or on the shape of the scales in Lepidoptera. Linden (1906), on the other hand, observed variations in the scales under the influence of humidity. Tower's (1906) investigations on the coloration of the potato beetle, *Leptinotarsa decemlineata*, Say, led him to the conclusion that humidity does not act directly on coloration, but on the rate of metabolic processes involved in the production of coloration. The amount of black pigment in the bug *Perillus bioculatus*, F., according to Knight (1924) does not depend on the air humidity.

Further examples of similar observations could be quoted, but this would not make the problem any clearer, since no exact quantitative work has ever been undertaken.

No experimental data exist on the influence of humidity on structural characters. With reference to the development of wings, suggestions have been made that a dry atmosphere favours the production of strong-flying forms, while a moist climate is favourable to brachypterism and apterism. There are, however, no experimental proofs of this theory.

The number of facets in the compound eyes of *Drosophila*, which is influenced by temperature (see p. 40), is not affected by humidity (Krafka, 1921).

(*c*) **Reproduction.**

A number of authors, working on different insects, have observed that the rate of reproduction is increased by higher percentages of relative humidity in the air.

The bean weevil, *Bruchus obtectus*, Say, enclosed in a sealed chamber, in which the air was desiccated by concentrated sulphuric acid had a greatly reduced rate of reproduction, a reduction of relative humidity to 26% preventing reproduction altogether (Headlee, 1917). Similar results were recorded by

Breitenbrecher (1918) with regard to the potato beetle, by Adolph (1920 for *Drosophila*, by Bacot (1914) for fleas, by Huber, Neiswander and Salter (1928) for the European corn-borer, and by Strachov-Koltchin (1915) for the grain weevil. (For other references see C. Robinson, 1925).

There are, however, some data of an opposite character, *i.e.* indicating an unfavourable influence on reproduction exerted by a high humidity. For example, Schubert (1928) records a falling off in the total number of eggs laid by the beet-bug, *Piesma quadratum*, Fieb., at a high humidity. The tsetse fly *Glossina palpalis*, R.-D., reproduces normally at 70% relative humidity, but a humidity of 100% arrests reproduction (Roubaud, 1909).

It will be seen that most of the data on this subject are rather vague and that exact quantitative data are very few in number. Moreover, no separate studies have been made on the influence of humidity on the development of sexual products and on oviposition, while the two processes may have different humidity optima.

(*d*) **Activity.**

Data on special activities as affected by the relative humidity of the air are reviewed elsewhere (see p. 93). No reliable information exists on the influence of this factor on the general activities of insects, apart from the observations on mosquitos made by Rudolfs (1923, 1924, 1925). The relation between the relative humidity of the air and the activities of mosquitos was found by this investigator to be less close than in the case of temperature. Up to 94–95% relative humidity, activity is accelerated, but on approaching the saturation point the activity experiences a sharp drop.

III. OTHER CLIMATIC FACTORS.

(*a*) **Light and Radiation.**

The influence on insects of light and radiation generally has received less attention than it deserves, and the existing data are mostly accidental, and scarcely any of them are quantitative. Data on radiation affecting the body temperature have been reviewed elsewhere (see p. 64).

(i) *Vital limits.*

It appears very doubtful whether light of very high intensity may be a direct cause of death in insects. Absolon's (1900) assertion that certain cave insects (*Dicyrtoma*, *Heteromurus*, *Tritomurus*) although blind are extremely sensitive to light and are killed even by a short exposure to direct sunlight must be treated with caution. While the observation itself may be correct, it is highly probable that death is caused not by the light, but by radiant heat, or by evaporation.

Examples of the fatal effects of radiant heat are very numerous, and one or two of them will suffice to illustrate the point. The eggs of the Mexican bean beetle, *Epilachna corrupta*, Muls., are killed by direct sunlight after an exposure of three hours at shade temperatures of 23–35° (N. Howard, 1924). Adults of the beetle *Melanotus communis*, Gyll., do not survive an exposure to direct sunlight if the surface of the ground is about 45–49° (Fulton, 1928). For further data see Uvarov, 1928; Pierce, 1926; Hinds, 1907; Sanderson, 1907; Stellwaag, 1925, 1927, 1928, 1929; Patterson, 1930; G. Carpenter, 1912, etc.

Many insects live and develop normally in an almost complete absence of light, *e.g.* soil insects, wood-boring insects, etc., though practically all of them pass at least one stage of their development (usually the adult) in the light. However, even insects that do not normally live in dark habitats can develop successfully in the absence of light, as has been proved by Northrop (1925), who bred *Drosophila* in the dark for 200 successive generations (see also F. Payne, 1910, 1911; Brannon, 1926). Sayle (1928) found that in the nymphs of the dragonfly *Aeschna umbrosa*, F. Wlk., the rate of metabolism was reduced by darkness and that the insects finally died. Death in this case, however, was apparently due to exhaustion.

Fatta and Mundula (1908) studied the length of life of starving beetles (*Carabus morbillosus*, F.) in darkness, and found that they survived for 260 days, instead of 301 days as in normal conditions.

Northrop made some interesting experiments on the effects of light of high intensity, with his culture of *Drosophila* bred in the dark (see above). He found that the larvae were killed by a continuous exposure to light of 7000–10,000 metre-candles. The pupae were killed by intensities above 5000 metre-candles. The duration of the life of the imago was markedly shortened by light of intensities above 1000 metre-candles (Fig. 20). This suggests that intensive light results in a "rate of ageing" proportional to the intensity of the light. Similar results were obtained by Barber (1925) with the adults of the European corn-borer moth, which lived for a shorter period under constant light than under normal conditions. No appreciable effect on the length of life was noticed in the moths subjected to constant darkness.

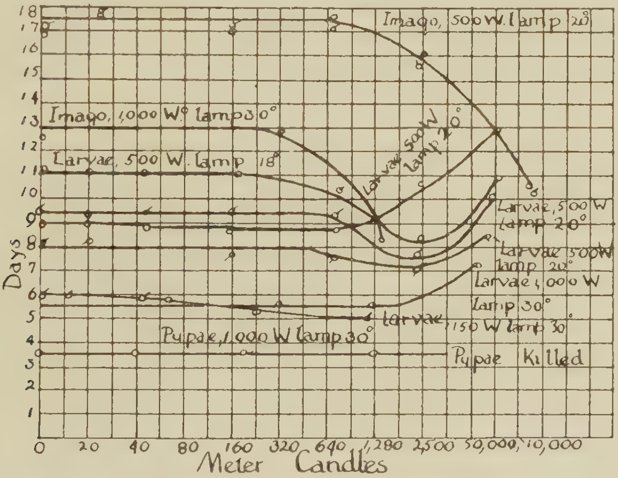

FIG. 20.—The influence of the intensity of artificial light on the rate of growth and duration of life in *Drosophila* (the duration of various stages in days has been plotted against the logarithms of the intensity of illumination in metre candles). (Re-drawn after Northrop, 1925.)

(ii) *Development.*

Data on development are both very meagre and contradictory. In Blunck's (1914) investigations on *Dytiscus marginalis*, L., the eggs were found to develop in complete darkness, but development took eight days longer than normally. Blunck, however, admits that it is possible that the effect was not directly due to the absence of light, but to the difference in the oxygen content of the water caused by the lack of light. Northrop (1926*a*) did not observe any difference between the duration of the larval and pupal periods of a normal culture of *Drosophila*, and that of the 230th generation of a culture kept in the dark. In Shelford's (1927) work on codling-moth pupae, the length of the pupal stage was invariably longer in the dark. Weidling (1928) has recorded that intensive electric light retards the development of larvae of *Calliphora* for about a week. (See also Friedrichs and Steiner, 1930; Rasseti, 1907; Sasaki.)

The influence of light of different intensities has been studied by Northrop (1925), who found that the larval period of *Drosophila* is shortened slightly at intensities of about 2500 metre-candles, but becomes increasingly longer at higher intensities (see Fig. 20). Barber (1925) made some observations on the rate of reproduction in the European corn-borer moth under different conditions of light. Moths subjected to constant darkness produced a somewhat larger number of eggs than the controls, while under constant light the average number of eggs was considerably reduced.

The emergence of insects from pupae appears to be influenced by light, since many of them emerge at a definite time of the day (Barnes, 1930; Bremer, 1926). Bremer attempted to influence the emergence by reversing the normal conditions of light and found that this affects the emergence of adults to some extent. The data, however, were not sufficient to prove that light was the main factor.

(iii) *Activity.*

The directive influence of light on insects, *i.e.* the phenomenon of phototropism, has been studied very extensively, but it constitutes a separate problem which will not be discussed here (see Mast, 1911). The kinetic effects of light, or its influence on the rate of general activities, are, on the other hand, still very insufficiently known. The stimulating effects of light on the activities of insects are evidenced by the fact that beetles of the genus *Chrysobothris* become active under bright weather conditions at 26°, while they remain inactive until 29° if the weather is cloudy (Graham, 1922; see also Minnich, 1920). F. Carpenter (1924) studied the rate of activity of *Drosophila* as influenced by light, and found that under a 250-candle arc light the muscle reflexes of the insect become very rapid and even violent. Moore and Cole (1921) studied the responses of the beetle *Popillia japonica*, Newm., to the light, in a quantitative way, and found that the rate of movement varies in proportion to the intensity of the light (Table XXX).

TABLE XXX.

VELOCITY OF CRAWLING OF *POPILLIA JAPONICA*, NEWM., UNDER LIGHT OF DIFFERENT INTENSITY. (After Moore and Cole.)

Intensity of light in metre-candles.	Time necessary to crawl 12·5 cm., in seconds.
85	15·50
234	13·14
608	11·60
1600	10·86
3276	10·22

The interesting, if not very exact, studies of Fiebrig (1912) on the " sleep " of insects, *i.e.* when they become inactive and are in a state of torpor, appear to show that this phenomenon depends on the conditions of light rather than of temperature, since " sleeping " Hymenoptera in his experiments did not react towards heat. The rate of respiration, which is indicative of the general metabolism, is higher in the light than in darkness, as has been found by Northrop (1926) for *Drosophila*, and by Sayle (1928) for dragonfly nymphs.

On the other hand, the general activity of some insects is definitely inhibited by light. Thus, many nocturnal insects become inactive under the influence of strong light, and this accounts, at least partly, for the inactivity of nocturnal insects in daytime (Chatanay, 1912; Kennedy, 1927). The problem has, however, never been studied experimentally (see also p. 99).

Some reactions of insects to other stimuli may be influenced by light. For example, the preferred temperature in light and in darkness may differ by several degrees (Bodenheimer and Schenkin, 1928). Larvae of *Tenebrio* exhibit under red light a stereotropic reaction, *i.e.* they crawl up a vertical glass plate, but a light of about 132 metre-candles and of a wave-length of about 535 $\mu\mu$ inhibits the stereotropism, and the larva avoids contact with the glass (Crozier, 1924, 1924*a*).

(iv) *Light of different wave-lengths.*

Practically all the above data on the influence of light refer to white light, whatever its source. The following are the not very numerous attempts that have been made to discover the more active parts of the spectrum.

There are only two papers on the influence of coloured light on the velocity of development. Schoch (1880) divided a batch of eggs of *Arctia caja*, L., into three portions, one of which was placed under red, another under blue, and the third under violet, glass. The caterpillars bred under violet glass developed more rapidly, consumed nearly double the amount of food and produced moths 14 days earlier than those under blue and red glass. Zhmuidzinovitch (1891*a*) experimented with silkworms, and found that the quickest development was obtained under blue light, while the rate of development decreased in the following order of colours : yellow, ordinary white, dark-violet, red and green.

Several authors have recorded data obtained on the effects of coloured light on the size of insects. The largest larvae of *Musca carnaria*, L., were obtained by Beclard (1858) when the larvae developed under violet light. Next in size came those bred under blue light, then those bred under red, yellow, and white. The smallest larvae, which were nearly one-third the size of the largest, were produced under the influence of green glass. In the case of silkworms, according to Gal (1898), it is again the violet light which favours their growth, the weight of cocoon, the amount of silk and the number of eggs laid by the resulting adults, all being greater than under normal light. Flammarion's (1899) data, however, show that ordinary dispersed light produces a relatively greater amount of silk per cocoon than any coloured light (see Table XXXI).

These results obtained by Beclard, Gal and Flammarion indicate that violet rays may produce larger individuals. This, however, is not an indication that these rays are generally more favourable for development, as has been suggested, since we know, for instance, that a low temperature may also produce larger individuals, though it retards their development. Linden (1899) was, therefore, probably right when she explained the fact that the largest adults of *Vanessa urticae*, L., were obtained under blue light, and

TABLE XXXI.

INFLUENCE OF COLOURED LIGHT ON SILKWORMS. (After Flammarion.)

Colour of glass.	Relative weight of silk per cocoon.	Ratio of females to males.	Relative weight of eggs per female.
Colourless	1	1	56
Purple-violet . . .	0·92	1·05	54
Orange	0·91	0·97	47
Pale green	0·90	0·98	53
Dark red	0·88	0·93	44
Pale red	0·88	0·95	50
Dark green	0·87	0·86	40
Pale blue	0·83	0·87	37
Dark blue	0·75	0·82	39

those of *Vanessa io*, L., in darkness, owing to the absence of heat rays in both cases. Reflected daylight, which is also poor in heat rays, produced larger adults of *Vanessa io.* It is true that in Schoch's experiments violet light was responsible for the greatest velocity of development, but these data are all very inexact, and it would be unsafe to draw any conclusions from them.

Flammarion (Table XXXI) found that the quality of light affects the percentage of the sexes, but Giard (1901) pointed out that sex is already determined in the egg, and that light acting on larvae cannot possibly influence it.

Other, but not more definite, data on the problem are quoted by Bachmetjew (1907), Shelford (1929), Martini and Achundow (1929), Kathariner (1901).

The influence of coloured light, acting on the pupae, on the coloration of adult Lepidoptera has been studied experimentally by Brecher (1918–1924*a*), Dürken (1923), Linden (1899) and Bachmetjew (1907), but the results are too indefinite to merit discussion.

(*b*) **Atmospheric Pressure.**

The first experiments on the vital limits of atmospheric pressure were made 260 years ago by Boyle (1670), who found that a vacuum did not affect caterpillars, while flying insects (flesh flies, ordinary flies, bees and wasps), a grasshopper, and a beetle, were killed by it.

Back and Cotton (1925) studied the problem from the point of view of the possible application of the vacuum to insect control. Short exposures to a 29-inch vacuum produced only a temporary effect, but longer exposures were fatal. After exposure the insects were stiff and brittle, *i.e.* thoroughly dried, so that death may have been actually due to exsiccation. Grasshoppers in Roller's (1906) experiments recovered after an exposure to a vacuum for 7 hours, but an exposure of 8 hours proved fatal.

The influence of a vacuum has been thoroughly tested by Lutz (1929), with the following surprising results. Fruit flies (*Drosophila*) were placed in a bell-jar with water and air exhausted to the vapour-pressure of water within 90 seconds. The flies stopped moving, but when the pressure was almost instantly returned to the normal, the flies walked about. Two of the flies survived this experiment repeated 24 consecutive times. A bumble-bee and two species of butterfly were subjected to a super-vacuum of less than one millimetre pressure for four minutes, and to that of 0·0001 mm. for 90 seconds, and then suddenly returned to the normal pressure. Only the butterflies died, the bumble-bee being unaffected. Gill (1921*a*) subjected the mosquito, *Culex fatigans*, Wied., to a reduction in pressure amounting to 6 inches, but neither the mosquitos, nor the malarial parasite in them, were affected.

The effects of very high pressure on insects were studied by Roller (1906), who submitted grasshoppers to a pressure of about 200 pounds (*i.e.* 13 atmospheres), and observed that they continued the respiratory movements, though at a reduced rate, for three days, after which they revived again under normal conditions. In order to stop respiration in 24 hours, a pressure of 250 pounds was necessary.

These results demonstrate that insects differ greatly in their response to atmospheric pressure from the higher animals and are able to tolerate enormous fluctuations in pressure, such as can never occur under natural conditions. This means that the ordinary changes in atmospheric pressure cannot possibly have a direct fatal effect on insects.

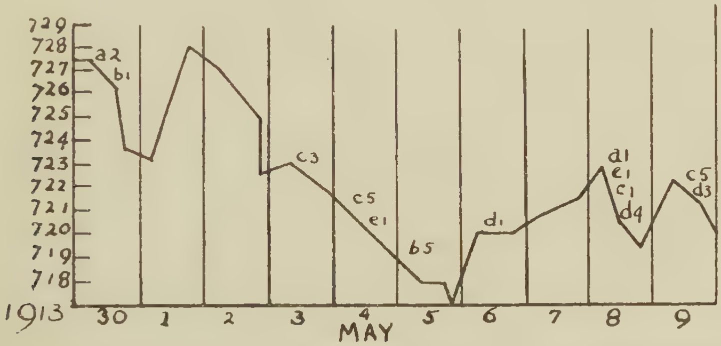

FIG. 21.—The emergence of Lepidoptera from pupae in connection with the barometric pressure. Letters a, b, c, d correspond to different species of Lepidoptera, the figure after each letter represents the number of individuals emerged. (Re-drawn after Pictet, 1917.)

It appears, also, that the rate of development of insects is not affected even by very considerable changes in the atmospheric pressure. Bataillon (1893) records some retardation of development in silkworms subjected to a pressure of 40–45 cm. of mercury. Rollat (1894) obtained indefinite results when subjecting silkworm eggs to a pressure of 3–4 atmospheres. Henneguy (1904) obtained the same results, though he observed that a pressure of 5–6 atmospheres delayed the hatching of mature eggs.

The last-mentioned observation by Henneguy has been repeated on Lepidopterous pupae by Petersen (1907), who noticed that the emergence of the adults coincides with the changes in barometric pressure. This idea was developed more fully by Pictet (1915*c*, 1915*d*, 1917, 1918, 1918*a*, 1918*b*), who came to the following conclusions based on observations both under natural and experimental conditions.

The action of a normal uniform pressure throughout the pupal period (pupae were placed under a bell-jar) prolongs the pupal stage. This is also observed if the pressure is made uniform at the end of the pupal period, when the adult is ready to emerge. The emergence can be delayed under these conditions until the insect dies in the pupa. A reduction of the pressure during the whole pupal stage shortens the pupal period, *e.g.* in *Pieris rapae*, L., at 710–728 mm. the stage lasted only 9 days instead of the normal 15 days. In nature, the emergence of adults in the majority of cases does not take place except on the fall of the barometer (Fig. 21), a reduction of the pressure by one millimetre being sufficient to cause the emergence of all adults, which are ready for it. If, however, a pupa is on the point of emerging when the barometer rises, the emergence is retarded until a new fall of the barometer. Pictet ascribes this influence of atmospheric pressure on emergence to a direct mechanical action, the adult insect being unable to burst the pupal skin until this becomes possible owing to the difference between the pressure of the body fluids and the outer air, resulting from a reduction in the atmospheric pressure. This explanation appears too theoretical, and requires checking by direct observations on the pressure of body fluids in connection with the pressure of the air.

The effects of atmospheric pressure on the activities of insects have never been studied quantitatively. There exist, however, a number of observations showing that the connection in this case is much more close than with development. These observations are reviewed in a later section (see p. 98).

(*c*) **Electricity.**

Very little experimental work has been done on the effects on insects of electrical discharges and currents. This influence is of a purely physiological interest, referring to such electric phenomena as are not likely to influence insects in nature (see a review in Bachmetjew, 1907). A few papers referring to the influence of electric states of the atmosphere on insect activities are reviewed elsewhere (p. 99), while here it may be mentioned that some authors (Bellier de la Chavignerie, 1858; Fallou, 1883; Lafitole, 1876) connect the appearance of aberrantly-coloured Lepidoptera with thundery weather during the period of emergence.

(*d*) **Movements of the Air.**

The rate of movement of the air has an important bearing on the rate of evaporation, but as a factor in itself, movement of the air can be of importance only in the mechanical destruction of insects (see p. 145), in their dispersal (see p. 116), or in exerting some influence on their activities (see p. 97).

IV. COMBINATIONS OF SEVERAL FACTORS.

An insect living under natural conditions is never exposed to one isolated climatic factor, but to the continually changing combinations of several. While in the study of the responses of an insect to environment it is necessary first to apply the analytical method, and to investigate the influence of each factor separately, it would be wrong to assume that the response of an insect to the combined action of several factors will represent merely a sum of the responses to each of the factors involved. Indeed, we must first satisfy ourselves whether this is true, or not, by studying experimentally all the more usual combinations of factors.

Unfortunately, as will be seen from the following pages, very little work has been done in this direction.

(*a*) **Heat and Humidity.**

(i) *Vital limits.*

There is a considerable amount of evidence to show that the same intensity of heat may affect an insect in a different way according to the relative humidity of the air, which in itself depends on the temperature. This refers particularly to the action of high temperatures.

Early experiments on the subject produced somewhat indefinite results. Thus, Kozhevnikov (1895–96) asserted that the humidity of the air has no influence on the resistance of insects to high temperatures, and Headlee (1916) came to a very similar conclusion. F. Cole (1906) observed that a high humidity of the environment at a temperature of 26·6° is very favourable for the survival of adult grain weevils, while the same temperature without moisture is fatal. Longevity of adult tsetse flies at 33°, according to Roubaud (1909*a*), is, in saturated air, six times that in normal air, and twelve times greater than in dry air. In Hamilton's (1917) experiments Carabid larvae, normally living in the soil, proved to be very sensitive to the relative humidity of the air, dying at 22·5° and 9% humidity within 115 minutes, while with the humidity at 64–95% an exposure to the same temperature did not affect the larvae. Kirkpatrick (1923) made extensive studies of the effects of air humidity on the resistance to heat of the cotton-seed bug, *Oxycarenus hyalinipennis*, Costa, and found that higher humidities increased the resistance. Thus, 100% mortality was reached at 25° after 150 hours' exposure if the humidity was 60%, but at 80% humidity an exposure lasting 300 hours was necessary to produce the same result.

In all these cases higher humidities proved to be favourable in the sense that they rendered the insect less susceptible to heat. There is, however, some evidence that this is not always the case. For example, Goodwin (1914, 1921), when studying the application of heat for the control of mill insects, found that in a practically saturated atmosphere the fatal point was 2–4° lower than in normal air.

It appears, therefore, that a simple general rule cannot be laid down. Indeed, the work of Pierce (1916) based on a very extensive series of experiments with the cotton-boll weevil, *Anthonomus grandis*, Boh., proved that there is a definite zone of the optimum combination of temperature and humidity, and that departures of each factor from this zone in either direction are injurious. Pierce prepared a full diagram (reproduced in Fig. 22), illustrating the various zones of activity and vitality of the weevil. This diagram shows at a glance the probable effects of every possible combination of the two factors, but there is little doubt that the relation is made to appear simpler than it actually is. Indeed, Shelford (1927) on the basis of his mass experiments with the codling moth constructed a chart of pupal mortality at different temperatures and humidities (Fig. 23), and the curves of the equal percentage of mortality show considerable irregularities. It is not clear whether these irregularities are due to the method of constructing the curves, or whether they represent the actual conditions. In any case, the idea of an optimum zone is fully corroborated by Shelford's data.

Similar results were obtained by J. Parker (1929, 1930; also Chapman, 1927) in his work with grasshopper eggs. The highest percentage of eggs hatched at 80% relative humidity and 22° temperature. At higher temperatures the humidity optimum was 90%. The higher the temperature, the

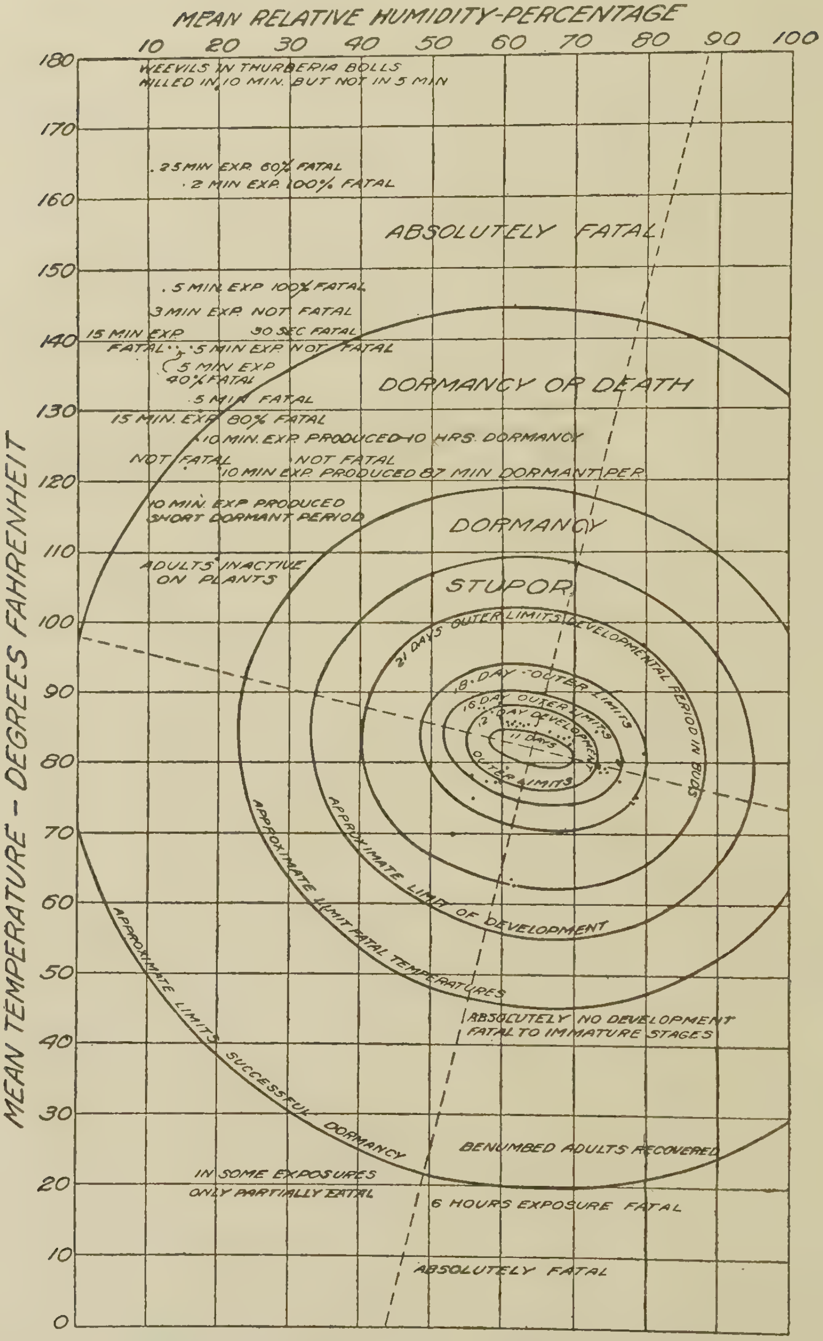

FIG. 22.—The influence of various combinations of temperature and humidity on the cotton-boll weevil. (After Pierce, 1917.)

narrower was the humidity range within which hatching took place. Thus, at 37° no hatching occurred except in humidities ranging from 70 to 100%, while at 22° hatching took place throughout the humidity range of 30 to 100%.

In Bodenheimer's (1930) work on the eggs of the Desert Locust, *Schistocerca gregaria*, Forsk., the optimum was at 30° and 100% relative humidity. The temperature limits were 25·5–33°, but humidities below 80% were injurious. His data are shown in Fig. 24.

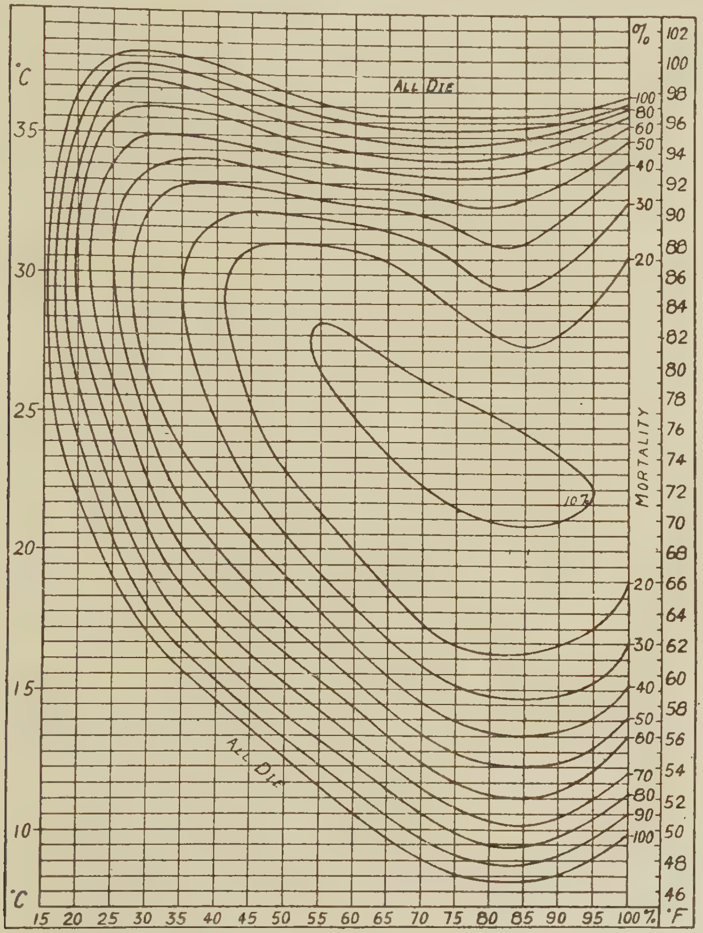

Fig. 23.—Equal mortality curves of codling-moth larvae at different combinations of temperature and humidity. (After Shelford, 1927.)

Some light was thrown on the physiological side of resistance to heat, as affected by the humidity of the air, by the recent work of Beattie (1928). This author found that the fly *Calliphora erythrocephala*, Mg., was least able to withstand exposures to high temperatures at humidities ranging from 60 to 80%, with an actual optimum at 70%. Both at the higher and at lower humidities the flies died even at lower temperatures. Since it is natural to suggest that death was due to the loss of water, determinations were made of the loss in weight. There was no loss at 90% humidity, and this suggests that insects die in saturated air because they are unable to control their body temperature by evaporation. The fatal effects of dry air are, however, less easy to understand, since the loss of weight was not greater in dry air than at 70% humidity.

The importance of the water balance in the body of an insect for its resistance to extremely low temperatures has already been discussed (see p. 12), and it is clear that any factor affecting the water balance is bound to influence the degree of cold resistance. Both the temperature of the air and its relative humidity are of primary importance in this respect, but no one has yet studied the relation of the water balance to the full complex of external factors.

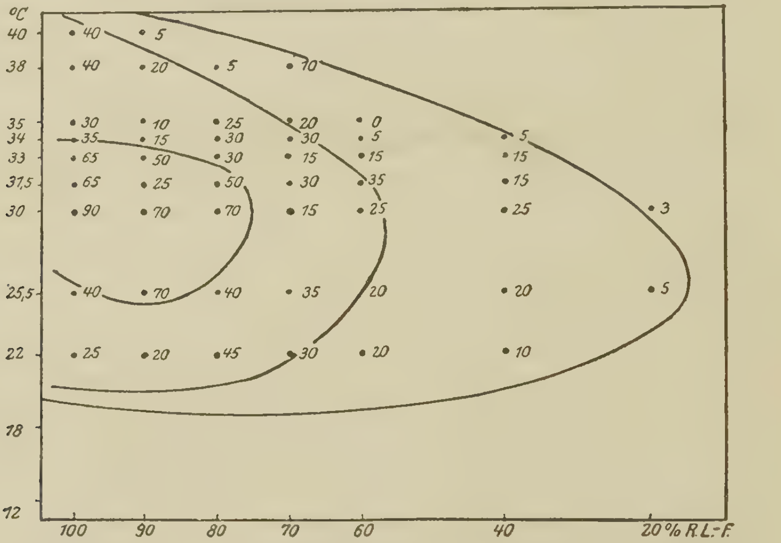

Fig. 24.—The mortality of eggs of the Desert Locust (in per cent.) at different combinations of temperature and humidity. (After Bodenheimer, 1930.)

(ii) *Development.*

The first fairly exhaustive studies on the combined effects of heat and humidity on the rate of development were arranged by Hennings (1907, 1907*a*; Pauly, 1906), who worked on the bark beetle, *Tomicus typographus*, L., breeding it at temperatures of 24°, 20°, 17° and 10°, and at relative humidities of 55% and 96%. His main conclusion was that air humidity has a decided inhibiting influence upon development at the same temperature. A lowering of the temperature by 3–4° extends the full life cycle of *T. typographus* by 15 days if the humidity is low, but at high humidities development may take more than 40 days longer than at the optimum conditions.

Titschak's (1925, 1927) work on the clothes moth led him to the conclusion that (1) development is inhibited by dry and warm conditions, (2) under moist and warm conditions it is accelerated, (3) under dry and cool conditions it is slightly retarded, and (4) under moist and cool conditions it is strongly retarded.

Weed (1927) working on the Aphid, *Myzus persicae*, Sulz., found that an increase in both the temperature and humidity accelerated metabolism, and that a reduction in both factors inhibited all metabolic processes.

According to Parker's (1929, 1930) experiments, hibernated grasshopper eggs showed interesting variations in the rate of development at different combinations of temperature and humidity. At a constant temperature of 27° the eggs kept at 60–100% relative humidity hatched in 10 days. Those kept at 50% hatched in 11 days; at 40% in 12 days; at 30% in 13 days; and no hatching occurred at 10–20%. In the case of eggs kept at 23–25°, the order of hatching was exactly the reverse, and the eggs at lower relative humidities hatched first. To explain this difference, Parker suggested that at the higher temperature the water content of the eggs kept at low relative humidities was reduced more rapidly than at lower temperatures, and that this reduction was responsible for the retardation of development. Here, therefore, we meet again with the fact that the response of the insect towards external factors depends on the water balance in its body. It follows that the balance must be studied in detail if we want to understand the action of the external factors.

The most extensive experiments so far made on the combined action of heat and humidity on the velocity of development are those of Shelford (1927, 1929), with pupae of the codling moth. His work was arranged primarily for the purpose of devising a method for forecasting the dates of the appearance of the various stages, and it is discussed later (see p. 181). Here it is sufficient to reproduce his chart (Fig. 25), showing equal velocity curves, based on one series of his experiments. The actual experimental data are shown on the chart by encircled dots, and one cannot fail to be struck by their scarcity. Indeed, one is justified in doubting whether the curves, arrived at mainly by calculations and graphic methods, express the actual relations between heat, humidity and the velocity of development. However, the curves appear to serve satisfactorily their purpose of indicating the velocity value for any combination of temperature and humidity, as is seen later (see p. 182), and this shows, that apart from details, they must be substantially correct.

(*b*) **Evaporation.**

The evaporative power of the air is the result of several separate factors, viz. temperature, relative humidity, air movement and barometric pressure. It has been suggested that by studying the responses of an insect towards evaporation we may be able to evaluate the influence of practically all the climatic factors. This idea was strongly advocated by Shelford (1912, 1913, 1914, 1914*a*), who in his papers presented some, mainly theoretical, considerations in its favour, and referred to some experiments, never published in full, which showed that the reactions of insects towards comparable rates of evaporation were similar, no matter whether the evaporation was due to dryness, temperature or to the rate of air movement. However, in his extensive experimental work on the codling moth, the same author (Shelford, 1927, 1930) found it impossible to use evaporation as a universal index of environmental conditions, and reverted to the study of temperature and relative humidity. Lathrop (1923) studied the correlation between evaporation and the rate of development in *Aphis pomi*, De G., and arrived at the conclusion that evaporation, as registered by the standard evaporimeter, is not a satisfactory index of insect metabolism. This is apparently due to the fact that the combination of factors which influence evaporation affects the rate of evaporation from the evaporimeter in a way differing from their effect upon living insects.

Some use has been made of the rate of evaporation with regard to insect metabolism and activities by Breitenbrecher (1918), Holdaway (1927) and

Huber, Nieswander and Salter (1928), but the data obtained do not indicate that the study of evaporation has any advantages over the study of the effects of isolated factors.

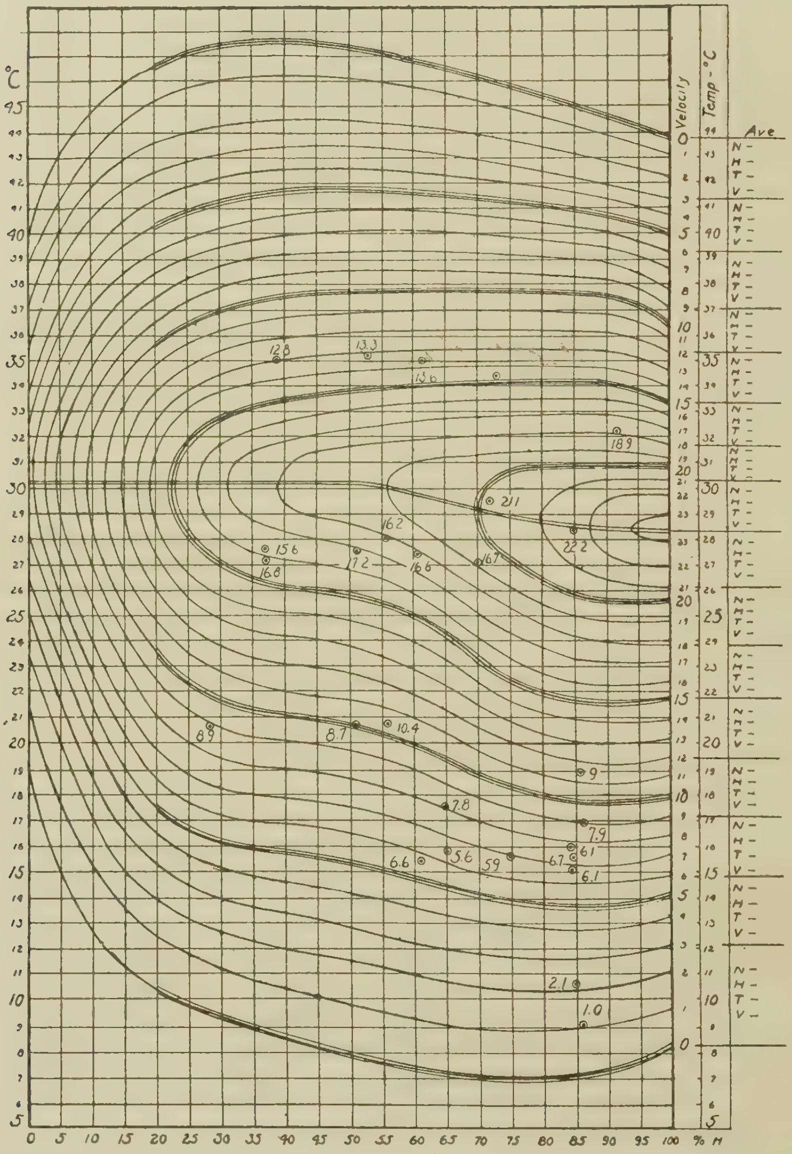

FIG. 25.—A velocity chart for the prepupal stage of the hibernated codling-moth larvae. Experimental data are shown by dots in circles, with the figures indicating the velocity. (After Shelford, 1929.)

PART II.

WEATHER, CLIMATE AND INSECTS.

V. RELATION OF WEATHER TO THE ACTIVITIES OF INSECTS.

The influence of the main climatic factors on the rate of the general activity of insects (see p. 56) have been reviewed in Part I of this paper. The present Part contains data on the correlation of various specific activities with actual weather conditions.

(*a*) **Temperature.**

(i) *Movements.*

The best-known example of the influence of temperature conditions on the movements of insects is offered by the mass migrations of locusts in the hopper (*i.e.* the larval) stage. Bands of hoppers of *Locusta migratoria*, L., begin to migrate when the temperature on the surface of the soil reaches 31·5–38°. A higher temperature is required to produce the same effect in the hoppers of later stages. The hoppers of the Moroccan locust, *Dociostaurus maroccanus*, Thunbg., start wandering at an air temperature of 23·5–27°. A rise of the temperature at ground level above 30° is necessary to induce the hoppers of *Calliptamus italicus*, L., to migrate (Uvarov, 1928; Nikolsky, 1925; Kiritchenko, 1926). Hoppers of the Desert Locust migrate if the temperature is between 27–40°. When it rises above 40°, the movement ceases (Bodenheimer, 1930; Fraenkel, 1929). Parker (1929, 1930) studied the temperature relations of the American grasshopper *Melanoplus mexicanus*, Sauss., and found that migration of hoppers begins at an air temperature of 21·7°, and at a soil surface temperature of 34·3°. For another species, *Camnula pellucida*, Scudd., the figures were 19·5° and 33·8°, respectively.

This direct connection between temperature conditions and the movements of locusts supplies an important clue to the understanding of their behaviour, and is of great value from the point of view of control measures (see p. 185).

The flight and migration of winged locusts are also closely dependent on temperature. According to Parker, the flights of *Melanoplus mexicanus*, Sauss., occur when the air temperature rises above 23·9°, the average temperature at which the flights were observed being 28·9°. Rockwood (1925) recorded a mass flight of various Acrididae during a very hot night, the air temperature being 31·6° at 8 p.m. and 25° at 11 p.m.

The dependence of flight on temperature conditions is also exhibited by other insects. The captures of night-flying Lepidoptera at light and in various traps have often been used as a method of studying the influence of weather conditions on activity, but the results, as far as temperature is concerned, are not uniform. Marchal (1912) summarised a large amount of data relating to the captures of vine moths (*Clysia* and *Polychrosis*) in light-traps, which showed that air temperature is correlated positively with the captures, but that other weather factors, particularly wind, have more effect. Ainslie (1917) found no correlation between the temperature of the night and the number of moths taken at light. M. Yothers (1926, 1927) studied the relation of the captures of codling moths by trap-baits to the average daily temperature, and obtained a very close correlation, as is shown in his graph (Fig. 26). The best study of this problem is that of Cook (1921, 1924*a*), who analysed statistically the influence of all weather factors on the captures of nocturnal Lepidoptera, at 65 bait traps during 3½ months. The temperature had a positive effect on the captures, its influence being much greater when the humidity was below the optimum. (See also G. Lehmann, 1904.)

Several authors have studied the correlation between temperature and the flight activities of other insects. They have usually found it to be positive (beetles, Chapman, 1923; Fenton and Dunnam, 1928; flies, Graham-Smith, 1916, 1919; leafhoppers, Lawson 1929). Rudolfs' (1922, 1923, 1924) work on the flight and general activities of mosquitos should be separately mentioned. This author reached the conclusion that air temperature is the deciding factor, activity beginning at about 10°, with the optimum range between 20 and 25°.

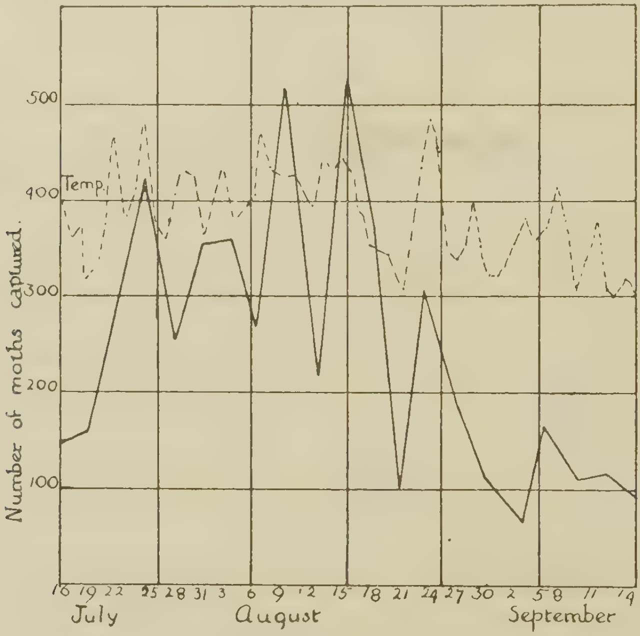

Fig. 26.—The effects of temperature (dotted line) upon the flight activity of the codling moth, as indicated by the number of moths captured in trap baits (black line). (Re-drawn after Yothers, 1927.)

A special case is presented by insects living in the soil. The temperature of the soil at different depths depends on a number of conditions, notably on the air temperature, the heat conductivity, which in its turn is connected with the physical structure of the soil, its humidity, etc. Soil insects, like all others, have a definite optimum and preferendum temperature, and the fluctuations of the temperature of the soil naturally cause the migration of soil insects from one layer to another. The problem has been recently studied experimentally by Handschin (1929), who found that as soon as the temperature of a given layer reaches 28–32°, the insects begin to move away, coming to rest in a layer with a temperature of 20–25°. Prinz (1928) investigated the relation of soil temperature to the movements of hibernating larvae of *Polyphylla olivieri*, Zap. The larvae live near the surface of the soil, but in autumn when the temperature of the soil at a depth of 20 cm. reaches 10–12°, the larvae begin to burrow more deeply. In spring they migrate to the upper layers, when the temperature at 20 cm. again reaches the same level (see Fig. 27). (On this subject see also McColloch and Hayes, 1922, 1923, 1928; Shelford, 1908.)

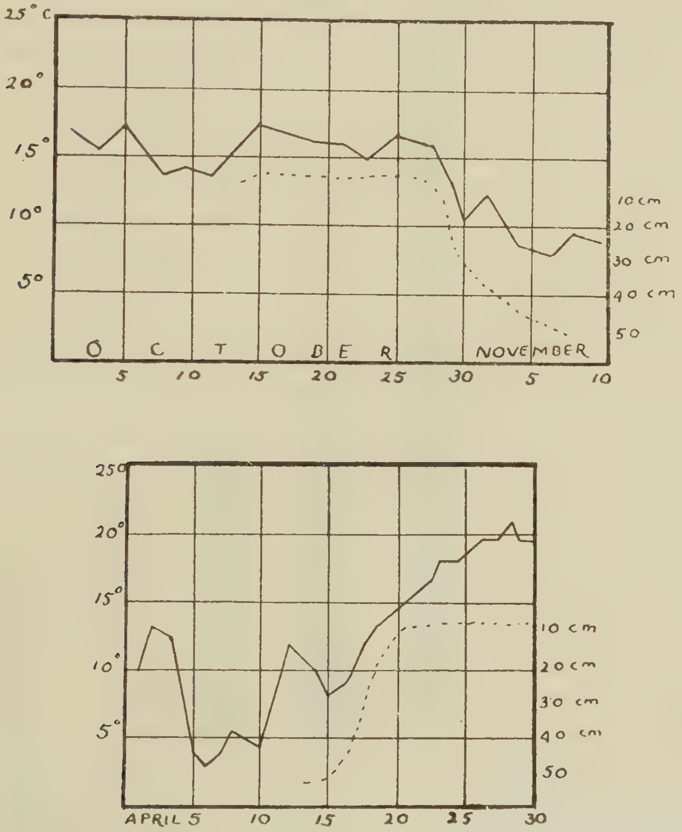

FIG. 27.—The soil temperature at a depth of 20 cm. (black line) and the movement of *Polyphylla* larvae in the soil in autumn and in spring (dotted line). (Re-drawn after Prinz, 1928.)

(ii) *Feeding.*

The amount of food taken by an insect, other conditions being equal, has an important influence on the rate of development, and any external factor affecting the amount of food taken becomes an indirect factor of metabolism. This brings out the necessity of studying the rate of the feeding activities of insects in connection with weather conditions. The problem has, moreover, a great practical interest, since the damage done by an insect is in many cases determined by the quantity of food taken by it.

The temperature limits for the feeding of each species are apparently very close to those for their activity generally. For example, the figures obtained by Parker (1929, 1930) for the temperatures at which the general activity of grasshoppers begins, and at which they start feeding, are almost identical.

A special case is presented by blood-sucking insects, in which feeding, while depending, like all other activities, on the air temperature, is determined by the temperature of the host as well. Under experimental conditions, mosquitos can be induced to bite any surface provided that it is sufficiently warm to provoke this response (Howlett, 1910; Marchand, 1918).

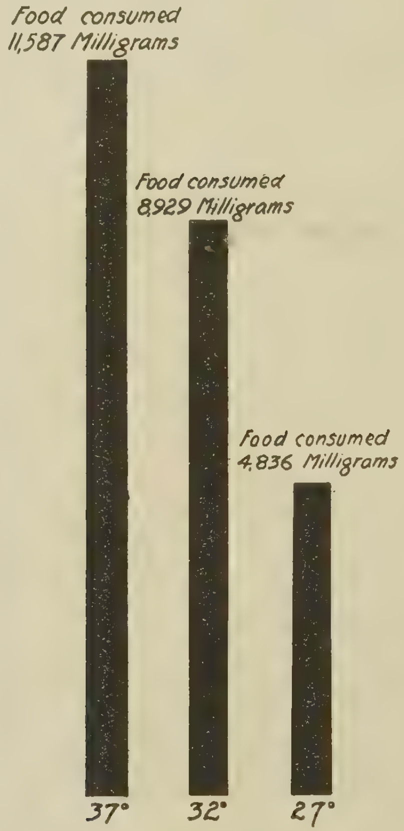

Fig. 28.—Total amount of food (dry weight) consumed by ten individuals of *Melanoplus atlanis* during the first 20 days of the adult life at different constant temperatures. (After Parker, 1930.)

Since heat, within the vital limits, increases the rate of all metabolic processes, it is not surprising that the amount of food taken is also increased in proportion with the temperature. This has been convincingly demonstrated by a number of authors, working with widely differing insects, viz. the cotton-boll weevil (Hunter and Hinds, 1904, 1905), Lepidopterous larvae (Regener, 1865; Bachmetjew, 1907; Mitchener, 1928), larvae of aquatic beetles (Blunck, 1923), Coccinellidae (Jöhnsen, 1930), locusts (Nenjukov and Parfentjev, 1929), and grasshoppers (Parker, 1929, 1930). Parker's observations on the feeding of grasshoppers at different temperatures are particularly complete, and Fig. 28 illustrates the connection very clearly.

There are, however, some exceptions to the rule, as has been pointed out by Pictet (1905) in the case of caterpillars after hibernation. Once their hibernation is completed, the caterpillars begin to feed, and feeding continues when the temperature drops even as low as — 1°. The quantity of food taken at 3–8° is equal to that consumed at 20°. Similarly, the moults of

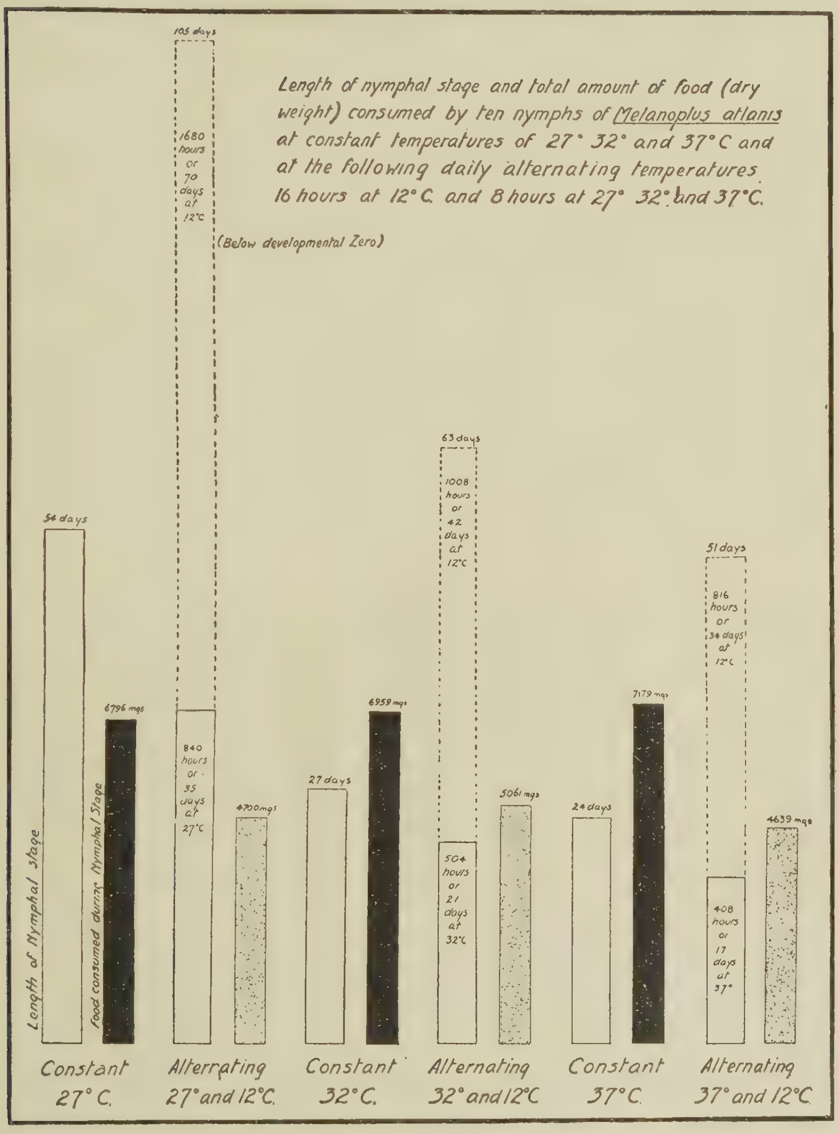

FIG. 29.—The length of development of hoppers of *Melanoplus atlanis* at constant and alternating temperatures. (After Parker, 1930.)

grasshopper larvae influence feeding activity, there being a decrease in feeding just before a moult, and an increase immediately after it, irrespective of the temperature (Parker, 1929, 1930). In both cases, we have to deal with an exceptional physiological state of the organism and these observations do not contradict the general rule that the amount of food taken increases with the temperature.

While feeding activity is thus closely connected with temperature conditions, a very different result is obtained when we consider the total amount of food necessary for complete development at different temperatures. Titschak (1925), when studying the development of the clothes moth, arrived at the somewhat unexpected conclusion that the total amount of food consumed by a developing larva is greater if the temperature is lower, and that a greater percentage of the food is absorbed, the quantity of excreta being less. Consequently, a greater percentage of the food is utilised for the building up of the tissues, and this accounts for the larger size of adults bred under cold conditions.

In Parker's investigations on grasshoppers the total amount of food taken by larvae remained practically the same at constant temperatures ranging from 22 to 37°, the increase in the daily amount of food at higher temperatures being counterbalanced by the shorter period of larval development (Fig. 29). It is very interesting to note that at alternating temperatures the grasshopper larvae developed on a smaller total amount of food than at a corresponding effective temperature, as will be seen from Fig. 29.

(iii) *Reproduction.*

There is little doubt that the copulation of insects is regulated by the temperature, but there are no exact observations on this point. Reh (1903–1904) recorded that the males of the scale-insect *Fonscolombia fraxini*, Kalt., may be observed searching for females at temperatures as low as — 4°, but this is, of course, an exceptional case of a very low limit of activity. Kirkpatrick (1923) observed that the cotton-seed bug, *Oxycarenus hyalinipennis*, Costa, is induced by high temperatures (25–40°) to copulate while in a quiescent state, but such copulation, without previous feeding, is never followed by oviposition.

The process of egg-laying also depends on the temperature. The temperature limits for oviposition are apparently fairly definite for each species. In the case of the tsetse fly, *Glossina palpalis*, R.-D., the reproduction (*i.e.* the deposition of mature larvae, the eggs of this fly developing to this stage within the body of the female) is possible only between the narrow limits of from 23° to 30° (Roubaud, 1909). In some Collembola, on the other hand, oviposition has been observed at 0° (Folsom, 1920). In Parker's (1929, 1930) observations on grasshoppers, the temperature limits for oviposition proved to be very close to the limits of general activities, and this probably holds good for most insects. Felt (1923), Garrett (1923), and Ilsey and Ackerman (1923) studied the relation of temperature to oviposition in the codling moth, and found that the evening temperature is the deciding factor.

That temperature has a positive influence upon the rate of reproduction, *i.e.* on the number of eggs laid per day, has been pointed out in a previous section (see p. 47). Supplementary data can be found in papers by Hunter and Hinds (1904, 1905), Strachov-Koltchin (1915), and Parks (1914). The last-named author obtained a very close correlation between the mean daily temperature, and the daily oviposition of the alfalfa weevil, *Phytonomus posticus*, Gyll., as shown in Fig. 30.

Again, as in the case of feeding, it is only the rate of oviposition which is accelerated by heat, but it is not clear whether the total production of eggs by a female is dependent on temperature, apart from the extreme temperatures inhibiting the development of the gonads.

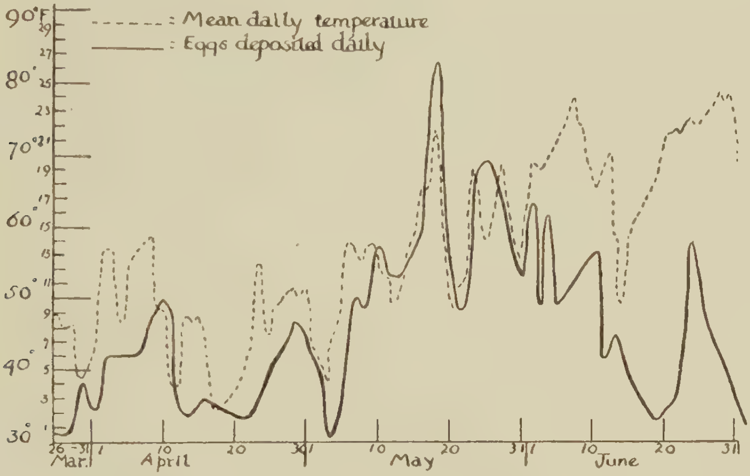

Fig. 30.—Effects of the mean daily temperature (dotted line) on the rate of oviposition of the alfalfa weevil (the black line represents the average number of eggs deposited daily by a beetle). (Re-drawn after Parks, 1914.)

(iv) *Stridulation.*

The production of sound by male crickets is connected with mating, and is, therefore, of considerable importance in the life of a species. Dolbear (1897) noticed that the rate of chirping, *i.e.* the number of movements of the elytra, is entirely dependent on the temperature, and the connection can be expressed by the formula

$$T = 50 + \frac{N - 40}{4},$$

where T is the temperature in degrees of Fahrenheit, and N is the rate per minute. Below 50° F. there are 40 chirps per minute, and above it there is an increase of about four chirps for each degree of temperature. Bessey (1898) corrected Dolbear's formula, since according to him the increase is not 4, but 4·7 chirps for each degree (see also Edes, 1899; Shull, 1907; Fulton, 1925; Allard, 1929).

(*b*) **Humidity.**

Data on the correlation between the various activities of insects and the humidity of the air are very meagre.

With regard to the flight of moths, the intensity of which can to some extent be gauged by the numbers caught at light, or in traps, some authors (*e.g.* Ainslie, 1917; Turner, 1920) believe that air humidity does not influence it at all. There is, however, some reliable evidence to the contrary. Prochnow (1905–6), for example, obtained a curve of the numbers of moths caught at light which agreed well with the curve of the absolute humidity of the air. He points out, however, that this may be partly due to the indirect influence of the temperature, since the absolute humidity, and the activity of the insects both increase with the temperature. Cook (1921), who studied the relative influence of the main weather factors on moth flight statistically, by means of correlation coefficients, found the relative humidity of the air to be the most important factor. Any increase in relative humidity up to about 54% tended to increase the captures of moths, but an increase beyond that value decreased the catch in almost the same proportion.

It is generally recognised that insect activity is depressed by low humidity. This fact has been recently emphasised by Dogel (1924), who, in quantitative studies of the insect population of meadow plots, observed that after a rain the population of the herb stratum increased to three times its former amount. He explains this by the fact that insects hide during droughts in crevices in the soil, etc., and emerge after the rain (see also Seamans, 1923). It appears, therefore, that this case must be considered as one suggesting the existence of a preferendum condition of humidity. During a drought suitable conditions can be found only in the soil, while after rain they exist also above ground. This temporary inactivity during a drought is a phenomenon of essentially the same kind as that of aestivation (see p. 108).

It is well known that mosquitos are more annoying when the weather is close, *i.e.* when both the relative humidity and the temperature are fairly high. Rudolfs (1923, 1924) published some exact observations on this subject, proving that the number of mosquitos alighting on a man increases in almost linear proportion with the increase in the relative humidity up to 85%. From 85 to 95% relative humidity, the number of alighting insects remains practically constant. The feeding of the mosquito, *Culex fatigans*, Wied., ceases altogether when the daily mean relative humidity is under 40%, while 50% humidity is favourable for feeding (Gill, 1921).

Buxton (1924*b*) suggested that the relative humidity of the air may play an indirect part in the activities of insects, owing to the absorption of the infra-red rays of the solar spectrum by the water vapour of the atmosphere (see below, p. 95). Another indirect influence exercised by humidity upon activity may be through its effect on the body temperature of insects (Bodenheimer, 1930; see also p. 63).

(*c*) **Precipitation.**

It is only natural that rain should interfere with the activities of insects, particularly with their flight. Apart from general observations, this has been proved by several authors who have studied the flight of moths (Marchal, 1912; Turner, 1920), and the activities of bees (Hambleton, 1925; Hollowell, 1929; Lundie, 1925; Munro, 1929; De Ong, 1925; G. Wilson, 1926). In the case of bees, rain was observed to check their flight even when the temperature was as high as 21° (De Ong, 1925). Many insects can be seen during rain in a state of torpor, or "sleep," clinging to plants. Fiebrig (1912) suggested that this state is due to the wetting of the wings, but this does not appear to be a satisfactory explanation. Certain insects, *e.g.* humble-bees (*Bombus* spp.) are not affected in their activities by heavy rain, or even by snow and hail showers, during which they continue to visit flowers. This disregard of weather conditions which are unfavourable to most insects, makes humble-bees very valuable as pollenisers (G. Wilson, 1926). Seitz (1891) observed that in Brazil some moths (*Macroglossa*) were active during rain.

Mist affects the flight of moths very unfavourably (Prochnow, 1905–6; Turner, 1920), probably because it occurs during cold nights. Some species, however, which can be active at very low temperatures, fly during misty nights (Rothke, 1913).

(*d*) Light and Radiation.

When one makes direct field observations on insects, it is practically impossible to separate the effects of light from those of heat, and there are scarcely any data in the literature that are absolutely reliable in this respect.

One of the first problems that arises in the consideration of the rôle played by light in the activities of insects, is presented by their division into diurnal and nocturnal classes. Since the diurnal insects are active only during the day, it is natural to suggest that their activity is stimulated by the conditions of light. Conversely, light may be supposed to inhibit the activities of nocturnal insects. The problem, however, is more complicated, and is discussed below (see p. 100).

It is hardly necessary to point out the stimulating effect of sunlight upon diurnal insects (see Graham-Smith, 1916; Bohn, 1907; Graham, 1922; Rudolfs, 1923; Wichmann, 1927), but there are no exact data to show whether the effect is due to the action of light, or to the raising of the body temperature by radiation. In any case, there is a definite positive correlation between the activity, for example, of honey-bees, and the hours of sunshine per day (Hambleton, 1925; Hutson, 1926). Lundie (1925) studied the effects of a storm on the activities of honey-bees (see Fig. 31). The main actual factors, interrupting their activities were the decrease in temperature and in the intensity of light. Although the temperature remained low after the storm, the bees resumed their activities. This shows that light must have been the principal factor. The activity of the ant, *Messor barbarus*, L., investigated by Buxton (1924*b*) proved to be inhibited between 9 a.m. and 3 p.m., *i.e.* when the sun was high, but the ants were active even at midday, if the relative humidity of the air was above 45%. Buxton suggested that the inhibition is due to the infra-red rays of the solar spectrum, which are cut off by the water vapour when the relative humidity is high.

So far very little attention has been paid to the influence of light on the feeding activities of insects, although the practical importance of evaluating all factors affecting feeding is obvious as far as the control of pests by stomach insecticides is concerned. The fact that insects appear to prefer light of a certain intensity and move accordingly, should influence the distribution of injuries between different parts of a plant. Thus, of two insects feeding on the foliage of a tree, one which is more photophilous will concentrate on the outside and upper branches, while another, preferring the shade, will feed on the lower branches, or on those nearer the trunk. Grevillius (1905) recorded, for example, that the larvae of the brown-tail moth, *Nygmia phaeorrhoea*, Don., always concentrate in the best-illuminated part of the cage, even if this part is kept cooler than the others. In other words, within certain limits (from 15·5° to 21·5°) temperature is of less importance than light.

The Potato Beetle, *Leptinotarsa decemlineata*, Say, while more active generally on warm, bright days, feeds more during the night than during the day. Under normal conditions a male eats 1·70 sq. inches of leaf surface in 48 hours, and a female eats 1·44 sq. inches, while the average area eaten by a beetle kept in darkness for the same period of time is 2·37 sq. inches (Gibson, Gorham, Hudson and Flock, 1925).

Turning our attention to reproductive activities as affected by light, we again find very few reliable data in the literature. Copulation in cockroaches can occur only in the darkness, and is inhibited by light (Wille, 1920). Oviposition by females of *Mantis religiosa*, L., on the contrary, is stimulated by light, since this insect starts laying eggs a few minutes after being exposed to the sunlight (Chopard, 1920). In this case, however, the effect may be also due to radiant heat. In the codling moth oviposition occurs usually in the evening, or at night. The controlling factor is the intensity of light, as shown by the experiments with moths kept in darkened cages. The optimum conditions for oviposition are at least a partial darkness and a temperature above 16·5°, so that no oviposition can take place if the night temperature is below that level, however warm the days may be (Isely and Ackerman, 1923). The fertility of the silkworm moth may be influenced by light, since in some Japanese experiments reviewed by Shelford (1929) the average number of eggs laid by the females reared in light was 569·2, while those reared "in shadow" laid on the average 635·0 eggs. The difference is not sufficiently pronounced for an opinion as to the importance of light on fecundity to be formed.

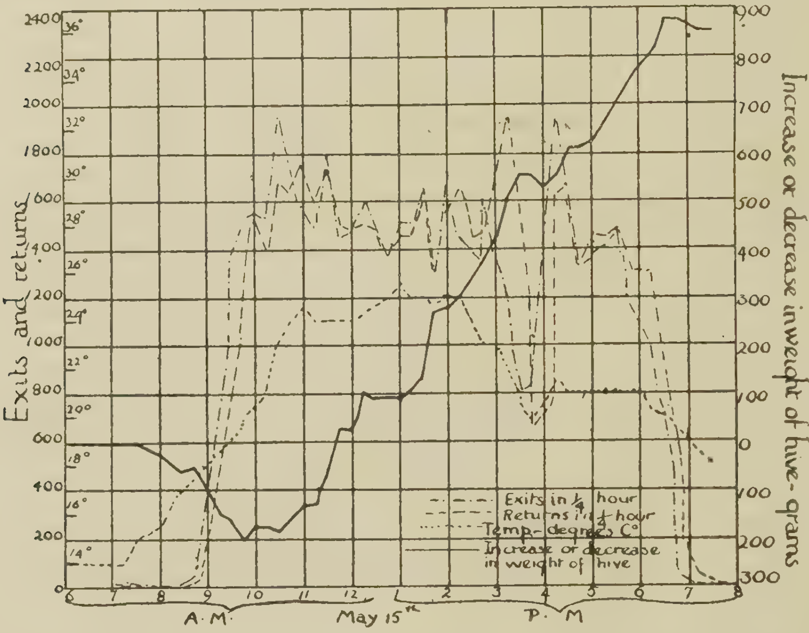

FIG. 31.—The effects of a threatened storm (between 2.30 and 4.15 p.m.) on the flight of honey-bees and the weight of the hive. (Re-drawn after Lundie, 1925.)

(*e*) Cloudiness.

It is scarcely possible to discuss cloudiness as a meteorological factor directly influencing insect activities, although there can be no doubt that clouds obscuring the sun are of great importance. This has been noticed, for example, with regard to locust hoppers, which stop their march even when the sun is obscured by a small passing cloud. This is due, apparently, to the sudden change in the intensity of light, or to the drop in the temperature (Uvarov, 1928; Parker, 1930). In the case of nocturnal Lepidoptera, cloudiness increases the numbers coming to light, but this must be due to the increase in the air humidity caused by cloudiness (Prochnow, 1905-6). The activity of honey-bees during cloudy intervals on sunny days is lowered. One bee visits, on the average, 9·6 flowers in a minute when the sun shines, and only 6·5 when there are clouds (G. Wilson, 1926). The actual cause remains unknown.

(*f*) **Wind.**

The flight of various insects is affected by wind very seriously. The velocity of wind that inhibits the flight of honey-bees has been estimated

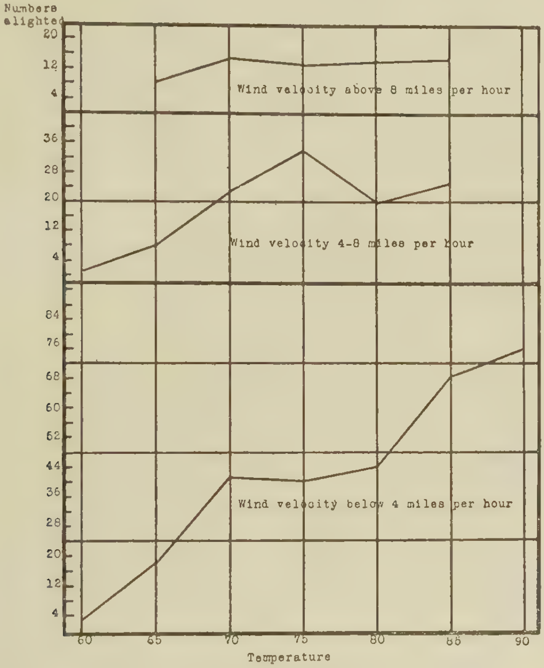

FIG. 32.—The influence of wind velocity on the activities of mosquitos as shown by the number of them alighting on a man. (After Rudolfs, 1923.)

differently by various authors, but is within the limits of 15–20 miles per hour. The flight of vine moths (*Clysia* and *Polychrosis*) is completely interrupted by wind, and even a slight breeze influences the catches more than do considerable variations in temperature (Marchal, 1912; see also Turner, 1920). The observations on the activities of mosquitos carried out by Rudolfs (1923) showed that the influence of wind upon the number of mosquitos alighting upon a man becomes apparent when the wind velocity reaches 4–8 miles per hour. At a wind velocity of 8 miles per hour, the rate of alighting remains constant, in spite of the increase of temperature, which means that the inhibiting influence of a strong wind is greater than the positive influence of a high temperature (Fig. 32). House-flies are also extremely sensitive to wind and seldom venture into the open on very windy days, even when it is hot (Graham-Smith, 1916). The same applies, to a probably still greater extent, to smaller insects, such as gnats (SIMULIIDAE), which can fly only if the air is calm, or almost so (Wilhelmi, 1920; Matthiesen, Peets and Dahlgrün, 1917).

All these data apply to flying insects, but wind may have a negative influence on the activities of insects living on the ground or on plants. Stäger (1928) recorded that a strong sirocco wind prevented the harvesting ants, *Messor barbarus*, L., from coming out of their nests. Fraenkel (1929) suggested that wind may be one of the factors determining the direction of mass movements of locust hoppers. Larvae of the beetle *Blitophaga opaca*, L., are very sensitive to wind and avoid exposed situations (Weber, 1928). These examples could be multiplied, but most of the observations recorded are not sufficiently exact to be of much use. It is desirable that more attention should be paid in future to the influence of wind on the activities of insects.

This influence may be of particular importance when it is concerned with the activities connected with reproduction, for flight in a great many insects is a primary factor in mating. This is very strikingly exhibited in the well-known phenomenon of the swarming of mosquitos and other small Diptera over tree-tops, steeples and similar objects. The insects often collect in such masses that they form a column resembling a cloud of smoke. This is undoubtedly connected with the convectional currents of the air, which are formed over tall objects in calm weather, and since the habit is connected with mating, the atmospheric conditions favouring the formation of convectional currents are of great importance to the species concerned (Gruhl, 1924, 1927; Knab, 1906).

(*g*) **Atmospheric Pressure.**

Sajo (1897) pointed out long ago that insects become unusually active during barometric depressions, when they move about and seek food and mates more energetically than at normal times. This connection between insect activity and depressions is known to seamen. Thus Schaupp (1879) recorded that the appearance of swarms of various insects off the South American coasts is considered by seamen as an indication of the approach of the *Pampero*, a S.W. wind which is, of course, preceded by a depression. According to Panow (1911) the appearance of the hawk-moth *Celerio livornica*, Esp., some miles from the shores of the Caspian Sea, during calm weather, is regarded by the local seamen as a sign of a coming north-east wind. The author himself had numerous opportunities of checking the accuracy of this view, and found that the moths always appeared some hours before the wind. Unfortunately, no barometric observations were made, but the connection of the flight of the moths with atmospheric depressions is clear. Similar observations were made in Egypt during the locust invasion of 1915, when on seventeen separate occasions the arrival of flying swarms of locusts in the Nile valley coincided with barometric depressions (Egypt, Ministry of Agriculture, 1916). Of course, it was not every depression that brought locusts with it, as a depression can only have that effect if it passes over a locality where there are swarms of locusts ready to migrate.

More exact studies on the connection between atmospheric pressure and the flight of insects have been made by Cook (1921), who studied statistically the correlation between weather factors and the number of moths caught in traps. The pressure was found to exert less influence on the number of specimens caught than either the temperature or the humidity. Similar observations by F. Hoffmann (1908) produced indefinite results.

Rhumbler (1926) put forward a suggestion that cockchafers (*Melolontha*) begin to fly in the evening owing to the usual slight (not over 0·1 mm.) rise in the barometric pressure which occurs every evening between 9 and 10 p.m., but the evidence in support of this view is not convincing.

According to Hering (1926), even the larvae of Lepidoptera are influenced in their activities by atmospheric pressure. He does not, however, present sufficient data to confirm his statement.

On the whole we must conclude that the influence of atmospheric pressure on the activities of insects remains at present practically unstudied.

(*h*) **Electric State of the Atmosphere.**

This subject has been even less studied than the preceding one. Marchal's (1912) data on the influence of the electric state of the atmosphere on the flight of vine moths tends to show that the insects are more active before a thunderstorm, and general statements to the same effect have been made by other authors writing on the subject of collecting moths at light or in traps. There are, however, no exact data, and it remains unknown whether the increase in the numbers of nocturnal insects flying before a thunderstorm is due to the electric state of the atmosphere, or to some other meteorological factor, *e.g.* pressure or humidity.

Gourdon (1929) stated that the ozonisation of the atmosphere during a thunderstorm causes insects to remain inactive for a long time after the storm, owing to the stupor produced by ozone. This statement requires corroboration.

(*i*) **Relation of Weather to the Activities of Bees.**

A number of authors have studied the influence of meteorological factors on the activities of bees collecting nectar and pollenising flowers. Such data from their work as is of general interest have been mentioned in this chapter. Those interested in this particular problem should consult the original papers by Ewert (1921); Hambleton (1925); K. Geiger (1925); Lundie (1925); Mitchener (1927); Fletcher (1909); Munro (1929); G. Wilson (1926); Kenoyer (1917); Nienhaus (1928); Romashov (1928); Waite (1895).

VI. DAILY AND ANNUAL CYCLES.

The more or less regular daily and seasonal changes in all weather factors cannot but have some influence on insects. The data summarised below show that this influence, while still very imperfectly understood, is undoubtedly very considerable.

(*a*) **Daily Rhythm.**

It is well known that some insects are active only in the daytime, while others only make their appearance at night. Moreover, every entomologist who has collected nocturnal insects knows that some of them come only early in the evening, *i.e.* at dusk, while others cannot be expected until very late. Still others fly throughout the night. The activities of diurnal insects are not equally noticeable throughout the day, some species being more active at midday, while others appear only towards the evening, etc.

There is scarcely any doubt that the daily activities of insects depend on the daily cycle of meteorological factors, but it is not at all clear which of these factors are primarily concerned.

(i) *Light.*

The suggestion that diurnal insects are active during the day because they are photophilous, while the nocturnal ones are photophobous, is the simplest that can be made. It does not, however, explain anything, but is a mere statement of an obvious fact.

There are very few exact observations and physiological theories on the rôle played by light on the activities of nocturnal insects. Chatanay (1912) put forward a suggestion that the inactivity of moths during the day is due to inhibition caused by light, and the same view was held by Kennedy (1927). The last-named author maintained that a strong light caused in nocturnal insects a state of catalepsy, or torpor, as a result of over-stimulation. Stockard (1908) experimented with a nocturnal stick-insect, *Aplopus mayeri*, Caud., and found that the beginning and the interruption of its activities were connected with the intensity of light, since the insects kept in a dark room continued moving all day. Similar results were obtained by Meunier (1928), who studied the swarming of the cockchafer, *Melolontha melolontha*, L. Under natural conditions swarming begins at dusk, and the time of its beginning changes from day to day, keeping pace with the change in the time of sunset (Fig. 33), so that it always coincides with a definite intensity of light, or degree of darkness. Under experimental conditions the beetles continue to swarm at the same definite hours, but it is possible to induce them to swarm at other times by artificial darkness. If the beetles are kept in the dark continually, the regularity of their swarming is lost.

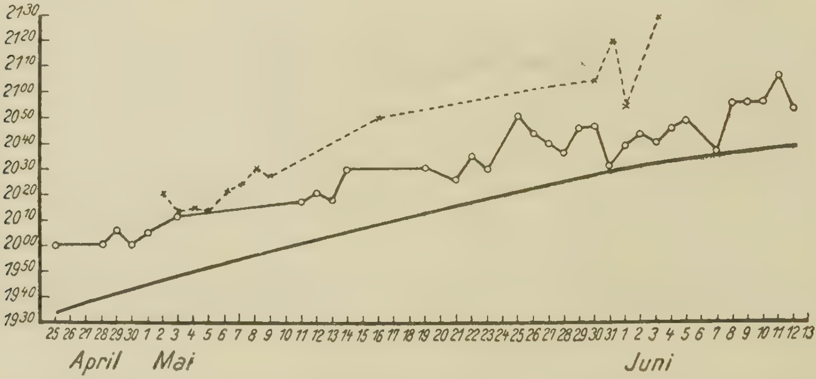

FIG. 33.—The relation of the swarming of *Melolontha* to the time of sunset. Dotted line, the times of the beginning of swarming in 1926; zig-zag line with circles, do. in 1927; black curve, the times of the sunset. Dates on the abscissa; hours on the ordinate. (After Meunier, 1928.)

While these observations suggest that the activities of nocturnal insects are directly dependent on conditions of light and do not represent a fixed rhythm, there is some evidence to the contrary. Roubaud (1918), for example, stated, that under laboratory conditions, the mosquito *Anopheles maculipennis*, Mg., remains motionless throughout the day and does not react even to abrupt changes from light to darkness, but at the beginning of natural twilight it suddenly starts flying and ceases its activity about two hours later.

Several authors (Weiss, 1913; Kennedy, 1927) suggested that the time of the activities of certain crepuscular insects, *e.g.* mosquitos, depends on the light being of definite intensity, but experimental proofs of this are lacking.

Herms (1929) proved by an interesting experiment that some nocturnal moths are active only in the absence of light. He kept a block of 15 apple trees lighted by means of six 500-watt Mazda lamps, suspended over the topmost branches of the trees, during the flight of the codling moth. The fruit from the lighted plot were affected by the pest in a lesser degree, and this shows that the lighting prevented the moths from oviposition. D. Collins and Nixon (1930) repeated the experiments with two other moths, and obtained similar results.

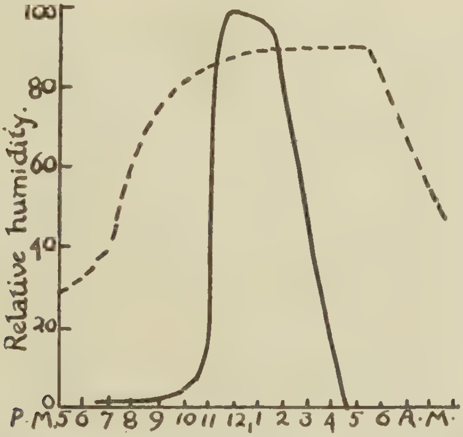

FIG. 34.—The influence of moonlight on the flight of moths (black line). Dusk from about 7 p.m., with a full moon until 10.45 p.m. (Re-drawn after Chatanay, 1912.)

Another argument in favour of the inhibiting influence of light on moths is that the number of moths caught at light and at baits is greatly affected by moonlight (see Fig. 34; Chatanay, 1912).

As regards the inactivity of diurnal insects at night, it is not at all clear that it is caused by the absence of light. Fiebrig (1912) insisted that the "sleep" of diurnal insects can be interrupted by light, but his experiments were not described in sufficient detail to be convincing. On the other hand, some insects of definitely diurnal habits, are, under certain conditions, very active at night. Thus, in hot climates, many ACRIDIDAE come to light (Rockwood, 1925; Uvarov, 1928), which shows that they sometimes fly at night.

Fraenkel (1929) in his studies on the daily cycle of the activities of the Desert Locust, *Schistocerca gregaria*, Forsk., came to the conclusion that some of them can be explained as reactions towards the light, but his data are not altogether convincing, and his explanations are somewhat artificial.

On the whole, the problem of light as a factor in the daily rhythm of insect activities requires further exact investigation.

Nothing is known of the influence on the development of insects of the daily fluctuations in illumination except some contradictory data on the production of sexual forms in Aphids, which are discussed later (see p. 113). Bremer (1926) paid some attention to the elucidation of the problem of the usual emergence from the pupae of diurnal insects in the morning, and of nocturnal ones in the afternoon. The reverse conditions of light affect the regularity to some extent, but it is not clear that light is the main factor (see also Verloren, 1862; Barnes, 1930).

(ii) *Temperature.*

Bachmetjew (1901*a*) maintained that butterflies fly in the day-time, and moths fly at night mainly owing to the difference in their body temperatures.

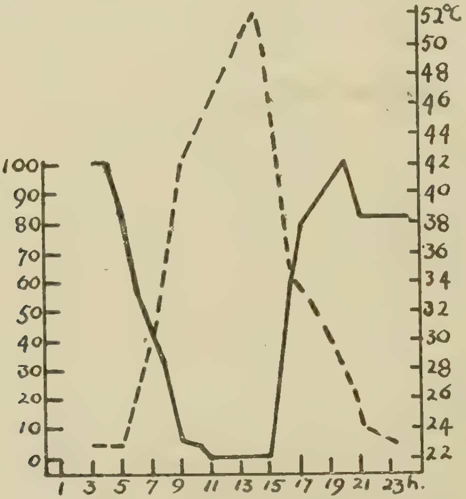

Fig. 35.—The relation of the temperature on the ground surface (dotted line) to the number of ants coming out of the nest (black line). (Re-drawn after Bodenheimer and Klein, 1930.)

Butterflies, the wings of which move slowly, are unable to raise the temperature of their bodies to a level which would counteract the low air temperature of the night, while moths make very rapid movements of the wings, and can, therefore, fly when the air temperature is relatively low. If, however, the body temperature were the only factor in the daily activities of insects, we should expect moths to fly in numbers during cool days, while butterflies would fly on hot nights. This does not happen, apart from some exceptional cases, and Bachmetjew's theory cannot be accepted as a general explanation of the daily cycle. At the same time, there is no doubt that cases of activity on hot nights of strictly diurnal insects, such as Acrididae (see above), are connected with the high air temperature, and consequently with the high body temperature. In other words, the temperature conditions may, in some cases, modify the normal daily cycle of activities to a considerable extent.

As regards the cycle of activities of diurnal insects as regulated by the temperature during the day, some work has been done on locusts (Nikolsky, 1925; Kiritchenko, 1926; Uvarov, 1928; Parker, 1924, 1929, 1930), and the results definitely show that practically the whole daily round, from the immobile night rest on plants, to the most energetic mass migration during the day, depend on the temperature conditions of the environment (air and soil temperature), and on the body temperature of the insects. Similarly, Bodenheimer and Klein (1930) found that the daily activity of the ant, *Messor semirufus*, André, is intimately connected with the soil temperature, with which it stands in an inverse ratio (Fig. 35).

The influence of daily fluctuations in temperature on the rate of development in insects has been very little studied, but the experimental data on the subject, reviewed elsewhere (see p. 33) suggest that this factor cannot be ignored. Parker's (1929, 1930) work on grasshoppers is particularly valuable in this connection, since he has established with a high degree of certainty that daily fluctuations of temperature are generally more favourable than constant temperatures for the development and growth of grasshoppers, which under such conditions reach the adult stage in less time and on less food.

(iii) *Humidity.*

Since the relative humidity of the air is subject to more or less regular daily fluctuations, it is natural to expect that the daily rhythm of insect activities may be connected with them. Picard (1912), Necheles (1927), and Martini (1929*a*) put forward a suggestion that nocturnal insects are active at night because they require a high degree of air humidity, and avoid excessive evaporation during the day by hiding in the soil and in crevices, etc. The idea is undoubtedly correct, but only to a certain extent, *i.e.* humidity is not the only factor that affects the daily cycle of insect activities. The simple argument used in the case of light proves this conclusion, namely that a damp rainy day does not bring out the nocturnal insects from their hiding-places.

(iv) *Atmospheric pressure.*

Rhumbler (1926), in his studies on the swarming of *Melolontha*, put forward a suggestion (*l.c.*, p. 174) that the beginning of swarming in the evening is due to the usual slight (not over 0·1 mm.) increase in the barometric pressure, which occurs every evening between 9 and 10 p.m. Since such small fluctuations of pressure occur at other times of the day and night without provoking the swarming of beetles, the view appears ill-founded, and the explanation of this phenomenon, offered by Meunier (1928) (see p. 100) seems more sound.

(v) *Conclusions.*

The above data, however meagre, are sufficient to show that the daily activities of insects are directly dependent on the daily rhythm of the weather. It appears that most activities are influenced by combinations of several meteorological factors. Attempts to explain the daily cycle by a single factor have very little chance of success (see also R. Hoffman, 1925).

A conclusive proof that the daily activities of insects do not depend on a fixed rhythm is offered by Newport (1837) in his unique observations on the activities of insects during a total eclipse of the sun on May 15th, 1836. At 2.15 p.m. when the eclipse began, and the sunlight was sensibly diminished, bees started flocking to the hives. At 3.15 p.m. when little light remained and the temperature dropped from 20° to 15°, the hive was quiet as in the evening, and a *Geotrupes stercorarius*, L., was noticed on the wing. Full activity was resumed at 4 p.m., when the eclipse was nearly over.

(*b*) **Seasonal Cycles.**

(i) *Generations.*

The length of time required for the complete development of an insect, from the moment when an egg is laid until the resulting adult lays eggs in its turn, varies in different insects. The relation of the time necessary to develop a generation to the annual climatic cycle is also variable. In the great majority of insects of temperate climates a generation develops within 12 months, and this appears also to be true with regard to many insects of the tropical climates, although surprisingly little has been published on this subject. There are, on the other hand, many species which require more than a full year for a generation to be produced. In these cases, a generation occupies a multiple of 12 months, *i.e.* 2, 3, 4 years, the longest known period being that of the American *Cicada septendecim*, L., which requires 17 years to complete its development. A similar example is offered by the cockchafers (*Melolontha*), which have one generation in four years in more northerly localities, and in three years in southerly ones.

A number of insects are able to produce several generations in a year, each generation taking only a short time for its full development. It might be supposed that such multivoltine insects, as they are called, would be more numerous in tropical countries, with their equable meteorological conditions, but there are not sufficient data to show that this is actually the case. In multivoltine insects of temperate climates, the generations only follow each other rapidly during the warm period of the year, while there is necessarily a more or less long period of rest during the winter.

Even in the simplest cases of univoltine insects the relation to the seasonal climatic cycle may present many variations, particularly with regard to the stage of development, which coincides with winter conditions. Amongst the European Lepidoptera, 66·9% of all species are known to hibernate as larvae, 4·3% as eggs, 28·2% as pupae and 1·5% as adults (Sajo, 1896*a*). The following table (Table XXXII; Escherich, 1914) shows how the 12 months' cycle of some common European insects may be divided between the various seasons. The heavily printed figures in the table indicate the duration of the hibernating stage.

TABLE XXXII.

SEASONAL LIFE-CYCLE OF SOME INSECTS. (After Escherich.)

	Duration of the stage in months.				
	Eggs.	Larva.	Pupa.	Immature adult.	Total.
Porthetria monacha . .	**9**	2·5	0·5	—	12
Sphinx pinastri . .	1	**10**	1	—	12
Panolis flammea . .	1	2·5	**8·5**	—	12
Pissodes	0·5	3	0·5	**8**	12

Summaries on life-cycles in different orders of insects have been published by E. Ball, Chapman, Folsom, Forbes, Fracker, Metcalf, Patch (all 1920).

We have to consider now to what extent the actual meteorological conditions of the various seasons may be regarded as the direct cause of one or other type of life-cycle in insects.

(ii) *Life-cycle and climate.*

The simplest case is that of the multivoltine insects which develop successive generations as long as the actual conditions (mainly temperature and humidity) remain favourable. Development may be temporarily suspended when the conditions become unfavourable. This may be due to the temperature dropping below the developmental zero, or to an insufficient amount of moisture, etc. The rate of development of the generations will, in this case, naturally vary with the conditions. The outstanding characteristic of this *homodynamic* (Roubaud, 1922, 1922*a*) type of development is the absence of a definite annual life-cycle, the number of generations in a year depending on the actual weather conditions.

Essentially different is the *heterodynamic* type, in which the annual cycle bears a more or less definite relation to the season and includes a resting stage usually coinciding with unfavourable seasonal conditions, though, as will be seen later, not necessarily directly dependent on them. This resting (or dormant) stage occurs either in winter (*hibernation*), or in the dry season (*aestivation*). The two cases are discussed separately.

(iii) *Hibernation.*

The fact that the hibernating pupae of certain species of Lepidoptera cannot be made to develop and produce adults merely by raising the temperature has long been known to collectors, who have tried to "force" the development of such pupae in order to obtain adults in winter. This has been confirmed in experimental investigations by a number of authors. Pictet (1905) recorded for example, that a considerably raised temperature, acting practically throughout the winter on hibernating pupae of *Mamestra brassicae*, L., did not reduce the stage by more than six weeks, which constitutes only one-fifth of the normal pupal period. Similar phenomena are known in the case of other hibernating insects. Thus, the grasshopper *Anacridium aegyptium*, L., hibernates in the adult stage, and the hibernating individuals do not mature sexually until the next spring, even if they are kept at a favourable temperature (Grassé, 1922). The eggs of various grasshoppers, hibernating normally in the ground, cannot be forced to develop by the application of a high temperature (Bodine, 1923; Uvarov, 1928).

Experiments have shown that, even when hibernation can be broken by high temperature, a high mortality results, or abnormal individuals are produced. This indicates that the heat, instead of merely accelerating the development, acts in this case as a factor disturbing its normal course. On the subject of the breaking-up of hibernation by high temperature see a review by Bachmetjew, 1907, and the papers by Acqua, 1923, 1924, 1925, 1929; F. Ball, 1901; Baumberger, 1917; Corte, 1922, 1923, 1923*a*; Dingler, 1925; Dobrzhanskii, 1922*a*; Gauckler, 1885, 1899–1900; Kalender, 1872, 1873; Luciani, 1885; Picard, 1923; Pictet, 1904, 1907, 1909, 1910, 1913, 1913*b*, 1915, 1916, 1921; Rühl, 1887; Sella, 1920; Suckow, 1827; M. Townsend, 1926; Verloren, 1862; Weismann, 1895; Wille, 1929.

Another proof that the state of hibernation is not a direct result of a low temperature alone, is offered by the remarkable fact, noted by Reaumur (1736), that many insects enter the dormant stage, *i.e.* begin to hibernate, when it is still quite warm. For example, the eggs of some grasshoppers are laid in early summer and are subjected during the summer and autumn to temperatures well above those at which the hatching occurs next spring. Caterpillars of *Aporia crataegi*, L., cease to feed and spin a "winter nest" as early as July. Inside this nest they remain inactive throughout the rest of the summer and the winter, continuing their development in the following spring.

Even in cases when the hibernating stage can be somewhat shortened by raising the temperature, a compensating lengthening of one of the next stages is observed. For example, if the hibernating caterpillars of *Lasiocampa quercus*, L., are kept at a temperature of 18°, they pupate in the middle of the winter, instead of in the spring, but the pupal stage becomes correspondingly longer, so that the adult emerges at the usual time (Pictet, 1904, 1910, 1913, 1915, 1921), and the normal annual cycle is restored.

A special case is presented by certain Lepidoptera, the adults of which emerge very late in the autumn and even in the early winter, e.g. *Operophthera brumata*, L. This moth displays a remarkable and unexpected geographical variation in the life-cycle, for the adults appear in Northern Russia in late September, in Central Russia at the end of October, in the Crimea at the end of November, in the Southern Tyrol in December, and in Sicily in January and February. In Switzerland the moths are on wing in the alpine area a month earlier than in the plains. It appears, therefore, that the pupal period of *O. brumata* is shorter at lower temperatures. Schneider-Orelli (1916) attempted to elucidate this puzzling case by experiments, but all his attempts to shorten by high temperatures the length of the pupal stage in the individuals from the plains of Switzerland, proved to be futile, while the application to them of low temperature lengthened this stage (see also Kusnezov, 1929).

All these facts suggest the existence in some insects from temperate climates, of a fixed seasonal life-cycle, which may be disturbed by abnormal temperature conditions, but cannot be easily suppressed by them. Some authors (Pictet in particular) are inclined to explain this phenomenon by natural selection, which would eliminate all individuals with the life-cycle not perfectly adjusted to the normal climatic conditions, but this suggestion is not supported by facts. On the other hand, some experimental data on the subject indicate that in this case there is no need to invoke the aid of natural selection, since the phenomenon can be explained by the direct, if not immediate, action of the environment. Pictet (1913) himself bred caterpillars of *Lasiocampa quercus*, L., at 22° for six successive generations, with the result that, while in the first generation all caterpillars hibernated normally when the time arrived, in the fifth generation 52% of the caterpillars were only inactive for one month, and 18·7% developed without hibernation at all and in the sixth generation practically all the caterpillars developed without hibernating. Under these conditions, the adults could be obtained at almost any season, instead of in July–August, when they emerge normally, although about 50% still tended to emerge at the usual time, owing to an adjustment in the length of the pupal period. Pictet used the results of his interesting experiment as an argument that the annual life-cycle is constant and hereditary, its origin being due to natural selection. They serve, however, to support even better the idea that the life-cycle of a species can be directly influenced by the seasonal climatic cycle. Indeed, since only six generations were necessary to produce a substantial change in the life-cycle, in adjustment to the new conditions, it is reasonable to suggest that a climatic cycle acting on a species for countless generations may make that species perfectly adjusted to it without the aid of natural selection. This adjustment to the normal seasonal cycle persists even under changed conditions, but can be broken if the new conditions become sufficiently constant. This theory (suggested by several authors, but more definitely formulated by Babcock, 1927*a*) postulates that the acquired response towards climatic conditions should be inherited. There is nothing against this admission, although, of course, the subject awaits further experimental investigations from this point of view.

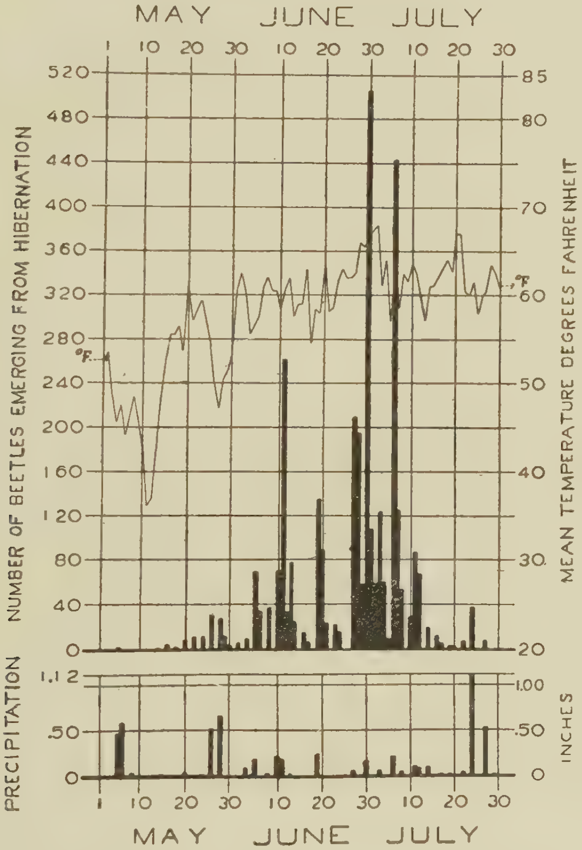

Fig. 36.—The emergence of Mexican bean beetles from hibernation in relation to precipitation. (After Douglass, 1928.)

Another important aspect of hibernation is the rôle played in development by exposure to cold in winter. The impossibility of forcing the development of hibernating insects by applying a high temperature, although development begins after an exposure to a low temperature, suggests that the latter may exert a stimulating influence. This suggestion is supported by experimental data, partly reviewed elsewhere (see p. 34, and Bachmetjew, 1907; Babcock, 1924, 1927, 1927*a*; Frings, 1899; Standfuss, 1896; Holmquist, 1928*a*; Regen, 1906; Sanderson, 1908). This paradox is discussed below (see p. 109).

The rôle played by temperature conditions in hibernation phenomena thus proves to be not as simple as would appear at first sight. There is, however, another factor, humidity, which must be taken into account. Standfuss (1896) pointed out that the pupae of *Saturnia* sp., which normally hibernate, can be made to develop by moistening them freely a number of times. In his experiments about 1% of the pupae so treated produced adults without hibernation. M. Townsend (1926) studied the conditions of the hibernation of the larvae of the codling moth and found that the greatest percentage of survival was obtained if the larvae were soaked frequently throughout the winter. Babcock's (1924, 1927, 1927*a*) thorough investigations of the hibernation of the European corn-borer, *Pyrausta nubilalis*, Hb., showed that the hibernating larvae are very sensitive to changes in contact moisture. Desiccation occurring during the dormant period results in the retardation of pupation. The normal end of the hibernation of the ladybird *Epilachna corrupta*, Muls., which passes the winter as an inactive adult, depends mainly on sufficient precipitation in spring (see Fig. 36; Douglass, 1928).

These data indicate that contact moisture is of very great importance in the process of hibernation. In the absence of moisture hibernation becomes longer than normal and is accompanied by a high percentage of mortality. An abundant moisture can even prevent hibernation completely. It is natural to suggest that in this case moisture is a factor directly affecting the water balance of the insect organism. Studies by Bodine (1921, 1923), Fink (1925) and Holmquist (1928), as well as of a number of authors who were interested in the relation of water balance to cold resistance (see p. 12), indicate that the period of preparation for hibernation is characterised by a reduction in the water content of the insect body, while the amount of water increases again after hibernation. This suggests that the reduction of water content may be regarded as an immediate cause of dormancy, while the absorption of contact moisture in spring may be a factor interrupting the dormant condition. On the other hand, the direct rôle of temperature conditions appears to be of secondary importance both in the inception of dormancy and in its normal end. A rise in temperature may sometimes supply a stimulus to the emergence from hibernation (Pokrovskii, 1922), but this presumably happens in the case of insects, which, though remaining in the hibernating stage, have already resumed their metabolic activity.

(iv) *Aestivation.*

Insects of dry countries are much more abundant and active in spring and autumn, while at the height of summer many of them are known to undergo a more or less long period of summer-dormancy, or aestivation. This is known definitely for a number of Chrysomelid beetles (Breitenbrecher, 1918; W. Kolbe, 1899; Sajo, 1896; Tower, 1906), and there are fairly numerous observations that this kind of dormancy can be prolonged very greatly if the dry conditions continue. For example, pupae of *Rothschildia jorulla*, Wstw., may produce moths 8 years after pupation (Rowley, 1923). Eggs of the Brown Locust, *Locustana pardalina*, Wlk., can be kept without hatching for 3½ years (Lounsbury, 1915). The Coccid *Margarodes vitium*, Giard, can be kept in an inactive state for 7, and even for as long as 17 years (Ferris, 1919; Mayet, 1896). A larva of a Longicorn beetle lived in the wood of a pencil box for 31 years (Gahan, 1924); etc. (see also Andrès, 1911; Giard, 1894, 1896, 1896*a*, 1902; Holtz, 1908, 1911; Marchal, 1897; Woglum, 1913).

Aestivation should be a common phenomenon in subtropical countries, with clearly defined dry and wet seasons, but so far no serious research has been carried out on the seasonal life-cycle of insects of such climates, at any rate from the physiological point of view. Some data on the subject of aestivation in the caterpillars of a rice-borer, *Scirpophaga innotata*, Wlk., which normally spend 4½ to 5½ dry months in a dormant stage have been published by Dammerman (1915). This author ascribed dormancy to dryness of the environment when the dry monsoon season sets in, but Goot (1925) believes it to be caused by feeding on more mature and drier plants. The last-named author found that aestivation occurred even if the fields were kept wet for several months. This, however, only proves the existence of an inherited seasonal cycle, which cannot be broken within a single generation. It is immaterial whether quiescence is induced by the dryness of the environment, or of the food. In both cases, a reduction in the water content of the insect should be expected, and this is probably the true cause of dormancy. In any case, the problem is a physiological one, and must be studied as such.

It appears that both hibernation and aestivation, which superficially might seem two directly opposite phenomena, are physiologically very closely allied and represent only special cases of a general phenomenon of diapauses, or temporary suspension of development. We now turn our attention to the discussion of general theories on diapauses in insect development.

(v) *Diapauses in general.*

Shelford (1929) suggested that the term dormancy or diapause (proposed by Henneguy, 1904), the two being synonymous, should be restricted to cases in which activity, or development, is arrested spontaneously. The cases in which activity, or development, is interrupted by the direct influence of unfavourable conditions, and is resumed as soon as the conditions become favourable, are referred to as quiescent stages, and do not come under the head of dormancy or diapause. The distinction may seem too fine and not always clear, but nevertheless it is sound theoretically, while the practical importance of clearly differentiating between the two classes of inactivity is obvious.

Diapauses may occur in any stage of the development of an insect. Embryonic diapauses are exemplified by the hibernating eggs of grasshoppers. The larval diapause in the rice-borer during the dry season has been discussed above. Pupal diapauses are a common occurrence in a number of insects hibernating in that stage. Imaginal diapauses occur in Lepidoptera (Pospelov, 1911), locusts (Uvarov, 1928), etc., and consist in an interruption in the development of gonads.

Not many physiological theories on diapauses have been advanced, and none of them is sufficiently convincing.

Roubaud (1922, 1922*a*, 1923, 1925, 1927, 1927*a*; Roubaud and Colas-Belcour, 1926) advanced a theory that diapauses are due to the self-intoxication of the organism by the excretory products (mainly urates), which cannot be eliminated as fast as they are produced when the rate of metabolism is high. A state of temporary inactivity at a low temperature (*athermobiosis*, in Roubaud's terminology), or at a low humidity (*anhydrobiosis*) is necessary to allow the excretory organs to purify the organism, which can then resume its development. This idea was expressed before Roubaud by Sajo (1896), who suggested that aestivation may be due to the accumulation of some substance inducing inactivity. Baumberger (1914) also suggested that hibernation may be due to the accumulation of inactive substances in the cytoplasm, causing a state akin to senility, and that the reduction in water content during hibernation results in a discharge of these substances and a rejuvenation of the organism.

The inactivity caused by the excess of excretory products is, according to Roubaud, a cyclical phenomenon in heterodynamic insects, and not immediately connected with the environmental conditions.

Roubaud's conclusions were based mainly on his experimental and histological studies of flies. His work has been criticised by Picard (1923) as being not equally applicable to the numerous cases of diapauses in Lepidoptera. Cousin (1929, 1929*a*, *b*, *c*, *d*,) in a series of papers published the results of her experiments on *Lucilia sericata*, Meig., one of the species on which Roubaud's theory was based, and concluded that diapauses do not correspond to the physiological purification of an organism, but are dependent directly on unfavourable environmental conditions, continuing only as long as the unfavourable factors exist. Since Cousin's experiments were made on one species of fly, it would be unsafe to generalise from their results, which are in contradiction to numerous data on other insects. Babcock (1927) attempted to apply Roubaud's theory to the hibernation of the European corn-borer, but found considerable difficulties in doing so and qualified the theory as one "supported by ingenious reasoning and equally ingenious, though not very exhaustive, experiments." H. Parker and Thompson (1927), again, failed to find any differences in the state of Malpighian tubes in hibernating and non-hibernating larvae of the corn-borer. On the whole, therefore, the theory of cyclical auto-intoxication causing diapauses and reactivation by athermobiosis and anhydrobiosis is not very popular amongst entomologists working on the problem.

M. Townsend (1926*a*) in his studies on the hibernation of the larvae of the codling moth suggested that the breaking-up of dormancy (see above) may be due to an enzyme requiring water for its action. Spooner (1927) studied the catalase content of larvae of the codling moth throughout a season, and the data obtained by him appeared to indicate some connection between the catalase content and dormancy. Such studies on enzymes are still in their earliest stages, and this accounts for the lack of definite results.

Heller (1926–1930) in a series of papers discussed the gaseous metabolism of Lepidopterous pupae, developing both with, and without, a diapause. He experimented with the hawk-moth, *Celerio euphorbiae*, L., which usually develops in one generation a year, pupation occurring in August–September, the pupa entering a diapause until the next spring. A certain percentage of the larvae, however, pupate earlier and the pupae develop without a diapause. Heller bred both kinds of individual through several generations, and came to the conclusion that the characteristic type of development cannot be influenced by temperature and is inherited as a Mendelian character. While his work is of the greatest interest to the problem, it is not possible to discuss it here, since it does not offer an explanation of the phenomenon of diapauses. Similarly, Decoppet (1920) insisted that the 3-year, or 4-year cycle of *Melolontha* in the different areas of Europe does not depend on climatic conditions, but that there are biological races of the insect, each with its fixed cycle. Zweigelt (1928) severely criticised Decoppet's theory (see also Tsukai, 1906).

To conclude, the problems of hibernation and aestivation, of diapauses and of the life-cycle generally, are still very far from being solved, although they are of great biological significance and of primary importance to the economic entomologist. The attention of research students should, therefore, be directed to the investigation of these problems. The work is not easy, since, as we have seen, the problems must be attacked from several different points of view. Experimental data will not suffice, unless they are supplemented by exact physiological and histological studies. In these, special attention should be paid to the difficult problem of the balance between free and colloidal water, as well as to the actual course of metabolism under different conditions.

The question of enzymes must also be considered, and special attention should be paid to the inheritance of acquired responses to climatic factors.

(vi) *Seasonal variation.*

Seasonal variation, or the existence of two or more different forms of a species, connected with different seasons, is best exemplified by certain butterflies that produce two generations a year, in which the adults of the spring generation differ strikingly in coloration from those of the summer one. The comparative study of the seasonal and climatic forms of Lepidoptera makes it possible to formulate the rule that the winter forms of seasonally dimorphic species agree in coloration with the local forms of the species occurring in cooler localities, while the summer forms resemble those of the warmer localities. This resemblance suggests that the differences between climatic and seasonal forms may be due to the same factor, namely temperature. Dorfmeister (1864) was the first to attempt, with some success, the artificial production of seasonal forms by applying high and low temperatures. A series of experiments by Weissmann (1875, 1895), Standfuss (1896), Merrifield (1890, 1911), Prochnow (1906) and many others, followed, and a great number of observations of unequal value was accumulated. A good summary of the literature on the subject was recently made by Prochnow (1926).

The main results, so far obtained, show that the colour forms of Lepidoptera appearing normally during the warmer, or the colder, season, depend on the action of temperature on their larvae and pupae. This action is regarded by most authors as indirect, *i.e.* that it merely releases a tendency to develop in a certain direction. The seasonal forms can be obtained by subjecting the pupae to the respective artificial temperatures, but in some cases the experiments do not succeed, *i.e.* sometimes the natural tendency of a pupa to produce a definite form cannot be suppressed by the reversed temperature. In other words, the direct influence of temperature is not always sufficient to change the normal rhythm of the generations.

Merrifield (1911) noticed that the effect of artificial temperature depends on the exact period of its application, and that the larvae when first hatched, can develop into either the winter or the summer form according to the temperature during their further development. In the later stages the natural direction of development becomes more pronounced and is less easily influenced by temperature.

A new light on the problem of seasonal dimorphism has been thrown by the interesting investigations of Süffert (1924, 1927), who has connected the phenomenon of dimorphism in *Araschnia levana-prorsa*, L., with the following type of development of the pupae:

(1) If the development of a pupa begins immediately after pupation and goes on at a medium temperature (15–30°) the summer form (*prorsa*) results. It is immaterial whether development without a diapause occurs normally or under the influence of artificial heat.

(2) If development does not begin immediately after pupation, and a

diapause occurs, the winter form (*levana*) is produced. If the diapause is complete, as in the case of hibernation, the typical winter form is obtained. A diapause of short duration results in intermediate forms. In this case, also, it is of no importance whether the diapause is natural, or produced artificially by lowering the temperature.

(3) The winter form (*levana*) can be obtained without a diapause if the development of the pupa is allowed to begin immediately after pupation, but goes on at a low temperature (between 0° and 10°) during a definite "period of susceptibility."

(4) It is, however, impossible to obtain the summer form (*prorsa*) after a diapause, even by the action of a high temperature.

Süffert's work has, thus, given an entirely new aspect to the problem of seasonal dimorphism. While previous authors studied the alternation of seasonal colour forms and the influence of climatic conditions on them, his work suggests that the solution should be sought in the study of seasonal cycles as affected by climate. In other words, the problem of seasonal dimorphism appears to be only a special case of the problem of cycles.

Seasonal dimorphism is not only exhibited in coloration, but in some other characters as well. In some species there is a considerable difference in the size of the seasonal forms, and this may be due to the different conditions of nutrition, since the larvae developing in autumn have a restricted supply of fresh green food and the resulting adults are of smaller size than those, the larvae of which develop during the spring and summer. Sometimes, however, the adults of the summer generation are smaller, and Standfuss (1896) suggested that this may be due to the shortening of the larval period of this generation owing to the higher temperature, so that the total amount of food taken is also smaller.

Differences in shape between seasonal forms are also known, e.g. *Heodes thersamon*, Esp., has tails to the wings only in the second generation. K. Jordan (1905) found a slight difference in the structure of the genital valves in the spring and summer forms of *Papilio xuthus*, L., but no difference was found in the genitalia of a series of other seasonally dimorphic species.

While temperature conditions are usually regarded as directly or indirectly responsible for the production of seasonal forms, Ruhmer (1898) put forward a suggestion that they may be due to seasonal differences in radiation. There are no data available to support this idea.

Seasonal forms in insects other than Lepidoptera have as yet been very little studied. China (1925) has proved by breeding, that the Capsid bugs *Notostira tricostata*, Costa, and *N. erratica*, L., differing not merely in colour, but also in the relative length of the antennal joints, represent the winter and the summer form, respectively, of a single species.

Some North American crickets, e.g. *Gryllus assimilis*, L., *G. pennsylvanicus*, Burm., and *Anaxipha exigua*, Say, hibernate partly in the egg-stage, and partly as larvae, so that there are two distinct broods of adults, in spring and in late summer. The adults of these broods differ very strikingly in their stridulation, and in the case of *Anaxipha* even in their habits, since the spring crickets live on the ground, under leaves, etc., while the summer brood crickets live on low-growing plants and shrubs. There are no structural, or colour, characters separating the individuals of the two broods, though there are obviously some deep physiological differences between them (Allard, 1929)

Michailow (1927*a*) calculated the constants of the tongue-length, the wing-length and width, and the length and hooks of the tergum, of bees emerging at five different periods in a season, and found considerable variation. This is, however, a phenomenon of a different kind and is probably directly connected with the nutritional conditions of the development of the larvae and pupae.

In the wild bees of the genus *Andrena*, which produce two annual generations, there are well-marked seasonal forms, the differences being more pronounced in the male sex (Perkins, 1919; Bischoff, 1927). In certain phytophagous Chalcids, *e.g.* in *Harmolita grandis*, Riley, the spring generation is wingless, while the summer generation is fully winged (F. Webster and Reeves, 1909). Picard (1919) described an interesting case of the Braconid *Sycosoter lavagnei*, Pic. & Licht., parasitic on *Hypoborus ficus*, Er., in which, although there are many overlapping generations in a year, there is a definite seasonal dimorphism. The winged individuals appear in the hotter part of the summer, while the wingless ones predominate in spring and again in autumn. A somewhat similar phenomenon has been observed with Aphids, in which the appearance of wingless and winged individuals is normally connected with the seasons (see below).

In Diptera, seasonal variation appears to be a very rare phenomenon, being known only in some AGROMYZIDAE (Hensel, 1870; Aldrich, 1918), and in two species of *Simulium* (Edwards, 1920). The spring broods of these species are paler and smaller than the summer broods.

The problem of seasonal forms in tropical climates has so far attracted attention only with regard to butterflies, and the work has been restricted mainly to proving, by breeding, the specific identity of the different forms flying during the dry and wet seasons. The phenomenon itself is very common in all climates where the difference in precipitation between the two seasons is sufficiently pronounced (Riley, 1925). In the tropical African PIERIDAE, for instance, there is hardly a species, which does not exhibit seasonal dimorphism. The genus *Precis* contains the most remarkable seasonally dimorphic species, e.g. *Precis octavia*, Cram., a bright red butterfly with strong black markings, which is the wet-season form of the blue and black *P. sesamus*, Trim., of the dry season.

Some preliminary experimental work on tropical African butterflies has been done by Marshall (1901; see also Dixey, 1906, 1907), and the results tend to show that seasonal forms in the tropics are connected with the influence not only of the temperature, but also of moisture. This is in harmony with Süffert's idea (see p. 111) that the production of seasonal forms is connected with the type of development, *i.e.* with the presence or absence of a diapause. We know (see p. 108) that diapauses may be caused by humidity, as well as by temperature (see also Manders, 1907*a*; Barker, 1895).

Some butterflies are said to offer examples of seasonal trimorphism, e.g. *Heodes phlaeas*, L., in Japan (Prochnow, 1906), but the case has never been studied experimentally.

(vii) *Alternation of generations in Aphids.*

Peculiarly complicated modifications of the annual life-cycle have been observed in some insects, in which individuals of different generations are dissimilar. Thus, in Aphids the parthenogenetic reproduction of apterous individuals can occur in a very long series of successive generations, but winged males and females usually appear at more or less definite periods of the seasonal cycle. This winged generation migrates, sometimes to an alternative food-plant. The factors causing the appearance of winged forms in Aphids have been studied by a number of authors.

The fact that parthenogenetic reproduction can go on for a number of generations if the environmental conditions generally are near the optimum, naturally suggests that the production of sexual forms may be due to departures of the conditions from the optimum.

The rôle of temperature in this connection has been studied experimentally by several authors (Wadley, 1923; L. Ackerman, 1926; Reinhard, 1927; Shinji, 1918; Shull, 1929), and the results are not all in agreement. Ackerman's work, however, supplies important physiological data which prove that temperature exerts a considerable influence on the production of winged, or wingless, forms. Particularly suggestive are his data on the influence of changes in the temperature stimulating the production of winged forms.

Marcovitch (1923, 1924), Shull (1928, 1929) and W. Ross (see De Gryse, 1929) paid attention to light as a possible factor in the production of winged forms. They found that Aphids bred in continuous electric light produced almost exclusively wingless offspring. The same result was obtained in continuous darkness. On the other hand, alternating periods of light and darkness acting on parents resulted in the appearance of winged offspring, the percentage of which depended on the length of the period of light. Practically all the offspring were winged when 8 hours of light alternated with 16 hours of darkness. Under such conditions it was possible to obtain a winged generation some months before it would normally appear in nature. The appearance of winged forms under natural conditions may be connected, therefore, with the relative length of day and night during the warmer season, the shorter days of the autumn favouring the production of the sexual generation. Davidson (1924) suggested that the influence may be indirect, acting through the light which affects the photosynthetic activities of the plant, the resulting changes in the sap serving as food for the Aphids. In some of Shull's experiments this has been taken into account.

The question of humidity has not been properly studied. Reinhard (1927) found no correlation between the relative humidity and the percentage of winged forms.

Some other authors who have discussed the problem of Aphid cycles generally, favour the view that there exists a fixed annual rhythm which can be modified only to a certain extent by external factors (Klodnitski, 1912; Ackerman, 1926; Uichanco, 1921; Patch, 1920). Davidson (1921) suggested that the appearance of wingless or winged forms is due to the segregation of the respective Mendelian factors, while external conditions may influence the metabolism of certain individuals, and thus indirectly affect the natural sequence of the chromosome segregations (see also Cazalis, 1870).

(viii) *Seasonal activities.*

Apart from cases in which an insect passes a season, or some part of it, in a diapause, differences obviously connected with seasons have been observed in the behaviour of fully active insects.

The approach of winter affects practically all insects, whether they hibernate in the state of a diapause, or are simply brought into a quiescent state by low temperature. During the summer the factors of food and breeding are the most potent ones in the activities of insects, but with the approach of cold weather most insects are driven from their usual habitats to some sheltered place, *e.g.* under stones, under the bark of trees, amongst fallen leaves, into the soil, etc. The insects normally living underground move still deeper (see p. 88).

This great autumnal migration of insects, causing a breakdown of the ecological distribution (Holmquist, 1926), is due to the influence of temperature, and also to some extent of moisture. In the spring a reverse process takes place. A knowledge of these seasonal migrations is obviously of the greatest value for the understanding of seasonal life-histories.

A somewhat similar phenomenon can be observed in dry and hot countries at the beginning of the summer, when the insects which do not retire for aestivation (see p. 108) have to concentrate in more favourable habitats. Thus, some grasshoppers in the Russian steppes migrate, at the height of summer, into the valleys of rivers where they can find abundant food, at a time when the steppe grasses are burnt up by the sun. In the autumn they return to the steppes for egg-laying. In Siberia, grasshoppers migrate in the second half of the summer from the fallow lands to the crops, while in autumn they return for egg-laying to the fallow lands, which are warmer (Vinokurov and Rubtzov, 1930).

In the tropics, where the main seasonal factor is the humidity and not the temperature, similar migrations of insect populations from one habitat to another should occur between the dry and wet seasons. Myers (1926) observed in Cuba that a Jassid, *Kolla similis*, Wlk., usually feeds on *Panicum barbinode* and on young sugar cane, but during the dry period this species occurs in numbers on a variety of plants differing in most respects, but growing under the conditions of greatest moisture which can be found during the drought.

Seasonal movements of tsetse flies in Africa are also connected with humidity, since the flies are extremely sensitive to it, and concentrate during the dry season near water. The actual migration coincides with the seasonal leaf-fall, which renders the humidity conditions in forests unfavourable to the flies (Roubaud, 1909*a*; Swynnerton, 1921; Jack, 1927).

Observations made by Dammerman (1925) on the soil fauna of the tropics revealed a close connection between the abundance of insects in the soil and the season. The population during the rainy season was 11–17 times as great as that during the dry season.

In the case of insects normally active throughout the favourable part of the year, there are also some fluctuations in activity connected with the season. Bodenheimer and Klein (1930) studied, for example, the activities of the harvesting ant *Messor semirufus*, André, in Palestine, during five seasons. The ants were active throughout the year, but the greatest activity was observed in April. Both in mid-winter and in mid-summer activity was at a minimum, in obvious correlation with a too low, or too high, temperature. It was interesting to note that the minimum temperature at which activity began differed according to the season, but without any definite relation to the outer temperature. This can be explained only by seasonal variation in the physiological state of the ants.

Studies on seasonal activities of honey-bees have been made by several authors (*e.g.* Kenoyer, 1907; Hambleton, 1925).

(*c*) **Lunar Periodicity.**

Hora (1927) noticed in India that swarms of mayflies appeared usually about the full moon period. He further studied the dates of the swarming of mayflies in other countries, and found in each species that the appearance of swarms coincided with a definite moon phase.

VII. CLIMATE AND DISTRIBUTION.

The area of distribution of a certain insect species is to a great extent the result of the geological history of the group to which it belongs, and this aspect of the problem does not come within the scope of the present work. This area, however, is not absolutely constant, since every species has a natural tendency to spread as widely as possible, but its dispersion is checked by certain limiting factors, which make it impossible for the insect to live successfully everywhere. Further, even within the normal range of the species it seldom occurs throughout it, but is usually connected with certain, more or less narrowly defined, habitat conditions. These conditions may be more favourable for the species in one part of its range than in another, and this results in the species being scarce in some parts, and abundant to the point of becoming a pest, in others.

Thus, the problem of insect distribution, as affected by climatic factors has to be studied from several points of view. It is necessary to ascertain which factors favour the dispersal of insects and which serve to set limits to it. Secondly, the requirements of insects as to the exact climatic conditions in various habitats should be studied in detail. Finally, from the economic point of view, it is imperative to consider the effects of local climates, not merely on the presence, or absence, of a certain insect species, but on its relative abundance, as well.

(*a*) Factors of Dispersal.

(i) *Wind.*

Isolated records of insects being carried by wind are fairly numerous, but no attempt has been made to collect them. It will be sufficient for our purpose to review only the papers of more general interest.

It would be natural to suggest that the most important factor in the passive dispersal of insects is wind of high velocity, *i.e.*, hurricanes and storms. This point of view has been stressed, for example, by Sajo (1897), while Müller (1871), Hunter and Hinds (1905) and Hunter and Pierce (1922) considered heavy windstorms, hurricanes and cyclones to be powerful agents in the spread of the cotton-boll weevil. Thus a series of cyclonic storms which occurred in May 1910 in the Mississippi area resulted in the appearance of many sporadic infestations by the weevil throughout the central parts of the State. Fletcher (1910) when studying the Microlepidopterous fauna of the Seychelles Islands suggested that tropical cyclones may play an important part in the dispersal of insects between oceanic islands, and Perkins (1913) thought that whirlwinds which often carry various small objects to a great height may assist in transporting insects from one island to another (see Felt, 1928; Hurd, 1920). Visher (1925–1926) quotes an interesting observation made by Dr. Wood-Jones on a swarm of hundreds of dragonflies brought by a severe hurricane to the Cocos-Keeling islands in the Indian Ocean from Sumatra, or Java, *i.e.* from a distance of 700 miles.

However, there is a considerable amount of evidence to show that more regular air movements of moderate velocity are probably of greater importance in the dispersal of insects than are hurricanes and cyclones. This problem has been attacked both with regard to the dispersal of certain species of economic insects, and in a general way.

The gipsy moth is one of the species for which wind dispersal is apparently of primary importance, since the larva has special aerostatic hairs enabling it to float in the air and to be carried even by a slight breeze for a distance up to 20–25 miles (Burgess, 1913; C. Collins, 1915, 1917; Felt, 1924; Minott, 1922; F. Shtscherbakov, 1914). Experiments with trapping the wind-borne larvae of the gipsy moth proved that wind is almost wholly responsible for the general spread of this insect in New England. The optimum wind velocity for its dispersal is 8 miles per hour, though the larvae have been caught at wind velocities ranging from 2 to 23 miles per hour (C. Collins, 1915).

Another example of insects spreading with the help of the wind is offered by the COCCIDAE, or scale-insects. Thus, young individuals of the black scale, *Saissetia oleae*, Bern., may be carried by wind, as is evidenced by their capture at tanglefoot screens, for considerable distances, up to 450 feet. In one case this scale-insect spread over an entire four-acre garden in a single season. The spread was chiefly in the direction of the prevailing winds (Quayle, 1916; see also Bondarev, 1928; F. Webster, 1902).

Tower (1906) studied the history of the dispersal of the potato beetle in the United States and concluded that the directions of the dispersal were determined mainly by the prevailing winds.

Plant-lice, or Aphids, although seemingly very fragile insects, offer some most remarkable cases of wind dispersal over enormous distances. Börner (1921) recorded that certain Aphids, which cannot breed continually on the island of Memmel because of the lack of their secondary food-plants, regularly arrive there from the Continent covering a distance of not less than 25 km. If a small island continually receives in this way a large population of Aphids, the total number of these insects carried away from the Continent must be enormous. The spruce Aphid, *Dilachnus piceae*, Panz., was found in considerable numbers on the surface of the snow at Spitzbergen by Parry's expedition in 1827, and again by Elton (1925, 1929) nearly a hundred years later. This Aphid lives on spruce (*Picea obovata* and *Picea excelsa*), and the nearest place where this tree grows abundantly is the Kola Peninsula, at a distance of 800 miles in a straight line. On the date when the Aphids were found by Elton, there were strong south-easterly winds blowing from Europe over Spitzbergen. These winds would transport the insects in about 12 to 24 hours. F. Webster and Phillips (1912) concluded from their studies of the grain Aphid, *Toxoptera graminum*, Rond., that its outbreaks in the United States have their origin in Central Texas, extending from there to the north and north-east in accordance with the direction of the prevailing winds. These authors point out that insects are liable to be carried by wind only if the temperature is above the lower limit of their activity.

McColloch (1917) studied the influence of wind on the dispersal of the Hessian fly and proved that fertilised females may be carried by wind for at least two miles.

Gnats (SIMULIIDAE) are often transported by wind from their breeding places and appear suddenly in great swarms elsewhere. This has been observed both in Europe (Tömösvary, 1885; Wilhelmi, 1920, 1921) and in America (F. Webster, 1902).

It is interesting to record that wind may be responsible for the dispersal of even such insects as are entirely unable to fly. Weber (1928), for instance, observed that larvae of the beetle *Blitophaga opaca*, L., can be carried by strong wind for considerable distances, and Schilling (1916; Nuttall, 1917) recorded that body lice, *Pediculus corporis*, L., have been observed to be transported by wind for a distance of 50 to 100 metres. The spread of infestation by the vine *Phylloxera* on the Rhine is in some cases due to the larvae being regularly transported by local winds (Wortmann, 1924).

General studies on insects carried by wind were arranged at some lighthouses by Clarke (1903), who recorded captures of various insects at the Kentish Knock lightship, which lies 21 miles from England and about 50 miles from the continent. Ball (1918) studied insects taken at the Rebecca Shoal light-station and recorded that mosquitos, house-flies and other insects were brought there by northerly winds from Florida, 105 miles away, and from Cuba, 90 miles away.

Felt (1925, 1925*a*, 1926, 1928, 1929), who collected all the literature bearing on the subject of the wind dispersal of insects, advanced a theory that an important part in the dispersal belongs to the convectional currents of the air arising from heated surfaces. Such currents carry insects with them to great altitudes, where the direction and the velocity of the wind may be quite different from those in the lower strata of the atmosphere. Insects carried by the upper air currents may drop when passing over some mountain tops, or large expanses of water, because there the descending currents are usually formed. In this way the presence of large numbers of insects on snow at high altitudes can be explained (see Hawkes, 1926; Humboldt, 1850; Tomlin and Sopp, 1901; Wheeler, 1917; Müller, 1871; and the criticism of Felt's theory by Williams, 1930).

The rôle of the upper air currents and of wind generally in the dispersal of insects is only suggested by the above records, and more exact and direct information as to the quantitative side of the problem is wanted. Indeed, it is not sufficient to prove that some insects may be carried by wind, for we have to know for which species this is a more regular way of dispersal. This kind of knowledge can be obtained only through systematically arranged investigations of the insect population of the different strata of the atmosphere. So far, practically nothing has been done in this direction. Studies of the aerial fauna of the lowest air stratum were organised by A. Bonnet (1911), who adjusted to the front of a motor-car a muslin net, with an opening of one sq. metre and recorded the numbers of insects caught in the net when covering one kilometre. This number would correspond roughly to the insect population of 1000 cub. mt. of the air. The average density of the population varied from 0 to 150 insects to 1 cubic metre, according to the time of the day, the temperature and the humidity of air. Unfortunately, no detailed accounts of this interesting work have been ever published and it is to be hoped that the idea will induce someone to carry out similar work in a systematic way.

Of considerable interest are the records of insects taken at a series of forest lookout stations (platforms raised above the tree-tops) in New Jersey collected by Weiss (1927). These records show that there is a considerable insect population, voluntary or otherwise, of the air above the level of the forest vegetation. Somewhat similar studies have been carried out by Felt (1929) by collecting insects on the roofs of tall buildings in the city of Albany, where approximately a thousand different species of insects belonging to various groups were taken, thus proving that the population of the respective strata of the atmosphere (over 100 feet above the ground) must be very rich and varied. The same author (1928) quoted some records of the captures of insects at an altitude of 2000–3000 ft., but these isolated data are too meagre to support his idea of the importance of the currents in the upper air in the dispersal of insects. The idea, while resting on a sound theoretical foundation, requires checking by extensive investigations carried out by means of aeroplanes, or balloons, with some adjustment for capturing insects at a known altitude. The value of such work for the better understanding of the dispersal of economic insects may be very great. This was realised by the Conference of Empire Meteorologists in London (1929), who adopted a resolution pointing out the necessity of organising studies of the insect fauna of the upper atmosphere. There is some hope that an attempt in this direction will be made in England before long.

Most of the above data and considerations refer to insects transported by the wind more or less passively, by drifting in the air currents. There are, however, many insects which migrate actively, being good fliers. Since this group includes a number of very important pests, locusts being a sufficiently convincing example, the influence of the wind on migrations and their direction must be studied. The influence of wind on the direction of the flight of locusts and grasshoppers has been discussed by many authors (*e.g.* Corkins, 1922; Lepiney, 1928; U. S. Entomological Commission, 1878, etc.), but no definite conclusions can be drawn. Very valuable data on the subject were accumulated by Lutz (1927), who recorded the insects taken in a special apparatus which consisted of eight traps placed in a circle round a lamp, each trap being always adjusted in the same position with regard to the wind. If the wind had no part in determining the direction of actively flying insects, there would have been about an equal number of insects taken in each trap. Actually, however, out of 10,000 insects collected in six weeks, 58·4% were caught in the three-eighths of the octagon that faced the wind, while the opposite three-eighths caught only 21·5%. This proves that most of the insects collected (mainly Diptera and Lepidoptera) tend usually to fly against the wind. With regard to the regularly migrating insects, Williams (1923*a*, 1926, 1930), who summarised the available information, found the evidence too contradictory for any definite theories to be formed.

Of course, in studies of this kind not only the direction, but also the velocity of the wind must be taken into account, as it cannot fail to affect the direction of actively flying insects, which may be able to fly against a slight breeze, but not against a wind of high velocity.

While discussing the influence of wind on insect movements it is necessary also to consider the atmospheric pressure which causes winds. The importance of this factor in the migration of insects has been discussed by several authors. Bartenev (1914) and Federley (1908) took barometric pressure into account when discussing migrations of dragonflies, but arrived at contradictory conclusions. Migrations of locusts in Egypt (Egypt, Ministry of Agriculture, 1916) have been noted as coinciding with barometric depressions, but Williams (1923*a*, 1926, 1930) failed to find in the literature on insect migration sufficient data for formulating a definite opinion as to whether atmospheric pressure has anything to do with the direction of flight. (For the data concerning the influence of atmospheric pressure on insect flight generally, see p. 103.)

(ii) *Temperature.*

Heat acts as a factor in the dispersal of insects only in an indirect way. We know (see Section V, p. 87) that the general activity of most insects increases with the temperature. When the temperature is below the zero of activity insects are in a state of cold torpor, hiding under bark, under stones on the ground, etc., or clinging to plants, and in this state they are most unlikely to be passively transported by the wind, while an active transport is, of course, altogether excluded. On the other hand, even non-flying insects are very active at higher temperatures and often climb to the tops of plants where they are liable to be carried away by gusts of wind. As for flying insects, they are most active in hot weather and a high temperature increases the chances of transport by wind. This connection between temperature and wind dispersal is illustrated, for example, by the observations of Collins (1915) on larvae of the gipsy moth, which become active and start crawling about at temperatures above 10°, when gusts of wind carry them off the plants. The optimum conditions for dispersal are at temperatures ranging from 18 to 30°. This is evidenced by the numbers caught by tanglefoot screens (see also Burgess, 1913; Webster and Phillips, 1912; Fenton and Dunnam, 1928; Rockwood, 1925; the literature dealing with the influence of heat on movement generally and on flight in particular should also be studied. For references see p. 87.

(iii) *Relative humidity.*

Since the relative humidity is a factor regulating the activities, including the flight, of some insects (see p. 93), it stands to reason that it is not without influence on wind dispersal, in the same way as is the case with temperature.

(iv) *Precipitation.*

There is no doubt that floods resulting from heavy rains or from the melting of snow in spring are responsible for the dispersal of many species of insects which are carried away by the water on floating tree-trunks, dead plants and other vegetable debris. For example, Hunter and Pierce (1922) have recorded that, in hilly areas, rain sweeps away immense numbers of buds and young cotton-boll weevils. These are carried by the running rain water for many miles, thus spreading the insect.

(*b*) **Limiting Factors.**

While the passive dispersal of insects by atmospheric agencies, as reviewed in the preceding paragraphs, is a very potent factor of distribution, the tendency of all organisms to spread actively is probably still more important in this respect. There is scarcely any need to present proofs that such a tendency exists. To quote only some of the more striking examples, swarms of locusts fly hundreds of miles from their breeding grounds, more often than not to perish from not finding suitable conditions for further propagation. Numerous records of migrations of butterflies and other insects, collected by Williams (1923*a*, 1926, 1930), show that migrations generally are of common occurrence. Most insects can either fly, or run, at least in one stage of their life, and this leads to an active dispersal, however short the distances may be, from the original birth-place. Even in the slowest-moving species the process of dispersal, either active or passive, continuing for countless generations, must inevitably lead to a theoretically limitless expansion of the area inhabited by the species. We see, however, that the faunas of different countries are not the same, and each species has a more or less definite area of distribution. There are, of course, some insects occurring practically all over the world, as for example the butterflies *Pyrameis cardui*, L., and *Danais plexippus*, L. The greatest percentage of cosmopolitan insects belongs, however, to the species which live in stored products and other merchandise, or in man's dwellings, and are, therefore, more or less independent of climatic conditions (see p. 136). Thus, the number of species which have so far proved capable of living under a wide range of climatic conditions is very small. It may be mentioned in this connection, that such species present a very interesting, physiological problem. Experimental studies of their responses to climatic factors would be worth undertaking. In such studies the possibility that individuals of the same species from different climates may differ physiologically should not be overlooked.

When an insect occurs only within a certain region, it is possible, and for an economic entomologist even essential, to subdivide the region according to the degree of the abundance of the species. Cook (1929) suggested the recognition of three different areas (he called them zones, but area seems to be a more suitable term), according to the degree of the destructiveness of the insect. The *area of normal abundance* is that within which the limiting conditions never, or rarely, occur, so that the insect is always present in considerable numbers and may be of economic importance every season. In the *area of occasional abundance* the insect is always present, but becomes a pest only in certain favourable seasons, when the limiting factors cease to exert their influence. In the *area of possible abundance* the insect is unable to maintain a permanent population owing to the annual, or almost annual, occurrence of limiting climatic conditions. Outbreaks in this area are rare and are due to the migration of the insects from one or both of the other two areas. To the three zones recognised by Cook, a fourth should be added, viz. the *area of specific distribution*, including the localities where the species occurs but is constantly kept in check by limiting factors and never becomes a pest.

We shall see now which of the climatic factors set limits to insect distribution. The next section, dealing with climatic control of abundance of insects in one locality should also be consulted in this connection.

(i) *Temperature.*

The northward distribution of insects in the Northern hemisphere is often limited by the annual minimum temperature. Thus, the northern limit of the Asparagus beetle, *Crioceris asparagi*, L., in North America agrees closely with the annual minimum isotherm of — 23° (Sanderson, 1908*a*). Similarly, the minimum isotherm of about — 35° determines the possible northern limit of the existence of *Nygmia phaeorrhoea*, Don., in Europe, because the larvae hibernating in nests are killed by frosts of about that intensity (Grevillius, 1905). We know that the survival of insects at low temperatures depends on the balance of the free and colloidal water in their bodies, and on their ability to retain or to adjust the balance during fluctuations of temperature (see p. 12). These inner factors of resistance should be studied in the case of all insects, the actual or possible limit of the distribution of which is required (W. Robinson, 1927*a*). This has not been done except in the case of one or two species studied by Robinson.

There are very few examples of insects being limited in their distribution by excessive heat. Bodenheimer (1928) has recorded, however, that the Cabbage White butterfly, *Pieris brassicae*, L., which reaches in Palestine its southern limit of distribution, can successfully breed in that country only during the winter, while in the summer months nearly 100% of eggs and young larvae are regularly killed off by the heat. Similar examples can be found in the literature of economic insects, but a direct correlation between the ability of an insect to withstand high temperatures and the data regarding the actual weather has in no case been established.

The data on the annual mean temperature as a limiting factor of distribution are more numerous. To quote only a few examples, Stellwaag's (1927, 1928, 1929) exhaustive researches on the European vine moths have shown that the optimum conditions for *Clysia ambiguella*, Hb., and *Polychrosis botrana*, Schiff., are the annual mean temperatures of 8·5–10° and 9·5–16°, respectively. For the tsetse fly *Glossina morsitans*, Wstw., the optimum mean annual temperature is approximately 26°, and the annual isotherm of about 20·5° presents the limit of its possible existence (Jack, 1927).

The mean temperature of the summer months, *i.e.* those of active life and development, is of importance in many cases. A study of the climatic conditions of the breeding areas of the Migratory Locust, *Locusta migratoria rossica*, Uv. & Zol., in Central Russia shows that their northern limit coincides with the summer isotherm 13·6° (Predtetchenskiĭ, 1928). An experiment in the application of temperature conditions to the study of the distribution of animals on a large scale, was made by Merriam (1892). He considered (on theoretical grounds) that animals are restricted in their distribution by the sum of daily effective mean temperatures during the active period. On the basis of this assumption he divided North America into three main regions, Boreal, Austral and Tropical. Merriam's idea has been applied, *e.g.* by Bodenheimer (1927*a*), to explain the distribution of *Hippotion celerio*, L., which requires 316·20 effective day-degrees for its development and cannot survive in countries where this sum is not reached during the summer months (see also Handlirsch, 1913).

(ii) *Humidity and Precipitation.*

If the temperature conditions of a region are favourable to an insect, it often happens that humidity plays the rôle of a limiting factor. In the case of the Migratory Locust referred to above, the mean summer temperature is the limiting factor only if the humidity is not too high. Where the mean relative humidity exceeds 73%, the breeding of the locust becomes impossible even if the temperature is within the optimum range (Predtetchenskiĭ, 1928). The absolute, and particularly the relative, humidity, plays a most important part as a factor in the distribution of Collembola, which are very sensitive in this respect. The degree of humidity is less important than, even small, fluctuations in it (Skorikov, 1899). In the case of one of these insects, *Sminthurus viridis*, L., Holdaway (1927) found that its distribution in Australia corresponds very closely to the area which receives an annual rainfall of 15 inches, and over.

(iii) *Combinations of factors.*

It appears that temperature and humidity (or precipitation) are the two main factors limiting the distribution of insects. Indeed, the controlling value of other climatic factors is relatively small and very inconstant (see p. 74).

Studies on temperature and humidity, or temperature and precipitation, as limiting the distribution of insects, can best be done with the aid of climatographs (see p. 123), and the work of Cook, who developed this method for use in entomology, is of particular interest. He applied it first (Cook, 1924) to an insect living in the soil, viz. the pale Western Cutworm, *Porosagrotis orthogonia*, Morr. Monthly means of temperature and monthly totals of precipitation were tabulated for all meteorological stations within the area where the outbreaks of this species occurred. The combined climatograph for all stations may be regarded as representing the optimum conditions for the species. This climatograph (Fig. 37) shows semi-arid conditions throughout the year, there being 1–1½ inches of rain in each of the three spring months, while the summer is hot and dry, the autumn drier than the spring, and the snowfall in winter light. On the basis of this climatograph and of the climatic data obtained at the various stations, a map (Fig. 38) was prepared, showing the

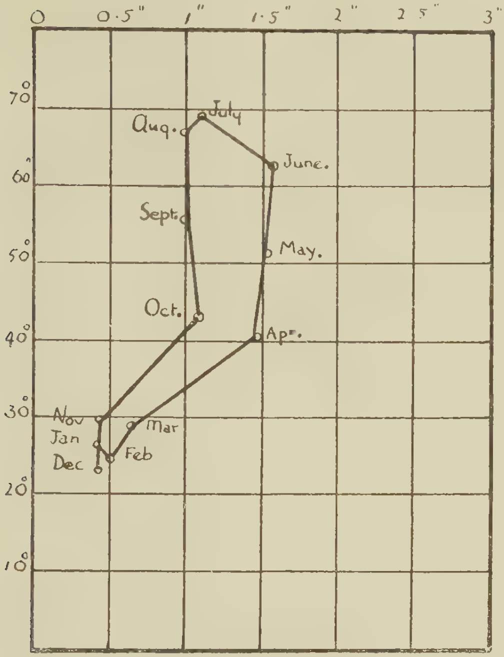

Fig. 37.—Climatograph of optimum conditions for *Porosagrotis orthogonia*. (Re-drawn after Cook, 1924.)

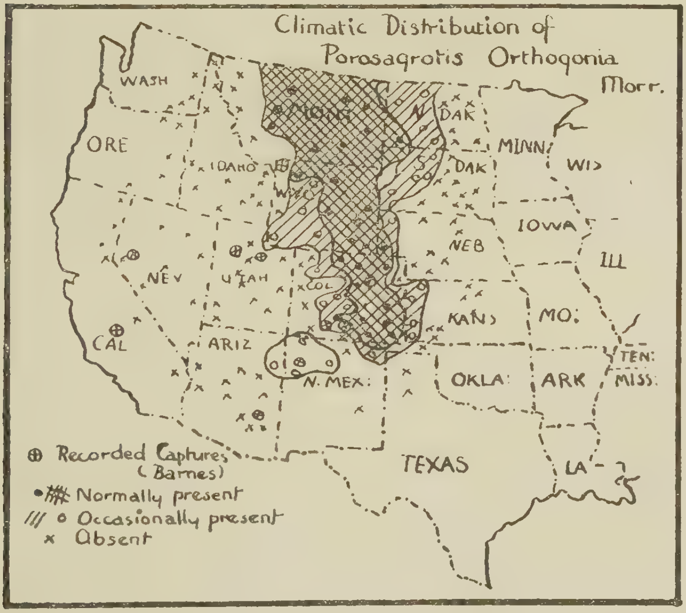
Climatic Distribution of Porosagrotis Orthogonia
Morr.
WASH
ORE
IDAHO
MONT
N. DAK
S. DAK
MINN
WIS
WYO
IOWA
NEB
ILL
NEV
UTAH
COL
KANS
MO.
CAL
ARIZ
N. MEX.
OKLA.
ARK
TEN.
MISS.
TEXAS
LA.
⊕ Recorded Captures (Barnes)
● ▩ Normally present
▨ ○ Occasionally present
× Absent

Fig. 38.—The distribution of *Porosagrotis orthogonia* in the United States. (Re-drawn after Cook, 1924.)

areas where the species was normally present, occasionally present, or absent. This map was found to agree closely with the actual conditions, apart from isolated captures of the moth outside the delimited area.

Again, the climatograph method proved useful in the study of areas in the United States, where damage from the alfalfa weevil, *Phytonomus posticus*, Gyll., can be expected (Cook, 1925). As this insect has been recently introduced into America, climatographs of several areas in Europe and in Asia, where it is a well-known pest, were studied and optimum conditions found. The optimum climatic areas in America were then defined. These proved to coincide with the areas where the infestation was noticed.

General studies on combined meteorological factors as limiting the distribution of insects have been made by many other authors, *e.g.* by Marlatt (1899) on scale insects; by Hunter and Pierce (1922) on the cotton-boll weevil; by Bodenheimer (1927) and by W. Robinson (1926) on the grain and rice weevils; and by Mansfield (1924) on the Colorado potato beetle. Studies of this kind are very useful for the proper analysis and understanding of distribution, but as the methods used are essentially the same as those employed in the studies on controlling factors it is not necessary to discuss them further.

(iv) *Fluctuations in the limits of distribution.*

The climate of any locality does not remain absolutely constant from year to year, but its component factors fluctuate within certain limits. As a result, the area of distribution of an insect is also never constant, but may extend one year and be restricted the next, owing to fluctuations in the limiting factors. There are, for instance, numerous records of the capture of rare southern insects in the northern countries of Europe, during, or after, exceptionally mild winters, or hot summers (*e.g.* a list of such captures of beetles is given by Meyer, 1909). Cook (1924*a*) made some very interesting studies of the composition of the fauna of moths at Bozeman, Montana, as revealed by catches at light during four successive years. The three dry years which preceded the first year of these studies increased enormously the proportion of the prairie elements in the fauna, while the eastern and the mountain species were reduced in numbers. During the following years the climate returned gradually to the normal, with the result that the prairie intruders were greatly reduced and some disappeared altogether, while the species of the other two groups assumed predominance.

These fluctuations in the area of distribution are closely connected with the problem of reservations which is discussed elsewhere (see p. 157).

(v) *Acclimatisation.*

Shelford (1929) in his recent book on ecology distinguishes between two conceptions, acclimatisation and acclimation. By the term acclimation is meant the adjustments in the constitution, or in the responses, of an individual animal transferred from one set of conditions to another. Thus, the process of the hardening of insects by the application of cold, or by desiccation, makes them acclimated to extremely low temperatures. The term acclimatisation is restricted by Shelford to cases when the adjustment to the new conditions is not individual, but several generations are required to bring about the change. Apart from the doubtful etymological correctness of the word acclimation, the term does not appear to be required. Indeed, acclimatisation to new conditions within a few generations cannot be expected to happen unless the first generation subjected to those conditions is able to survive, and moreover, to reproduce its kind under them. This can only happen if the individuals of the first generation become changed in a way which would enable them to withstand the new conditions. Thus, the difference between acclimation and acclimatisation in Shelford's sense is purely formal.

The ability of a species to adjust itself to new environmental conditions is very important, since it enables the species to expand the area of its distribution. From the economic point of view, the problem is important in the case of pests, introduced, or likely to be introduced, into a new country, and in the case of parasites transported from one country to another for biological control. So far, however, very little work has been done on this subject.

The gradual spread of the cotton-boll weevil from Mexico to the United States offers a good example of acclimatisation. It was thought at first that the beetle, coming originally from a southern climate, would soon be checked in its distribution by the temperature factor, but the insect proved to be capable of adjusting itself to new conditions, and its northward range has been gradually extended (Hinds, 1907).

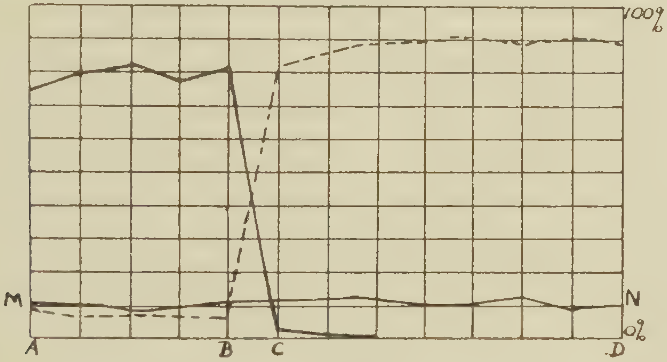

Fig. 39.—Graph showing the percentage of potato beetles surviving hibernation (black curve), eliminated before (curve MN) and during hibernation (dotted curve). The section A–B represents conditions in the original habitat, Chicago; C–D, conditions in the same habitat, but in the case of beetles which were returned to Chicago after being subjected to dry desert climate of Arizona for several generations. (Re-drawn after Tower, 1917.)

Acclimatisation to humidity conditions has been studied by Tower (1917) and by Breitenbrecher (1911, 1918) in the potato beetle, *Leptinotarsa decemlineata*, Say. Colonies of beetles from the Chicago area were transferred to the desert climate of Arizona, and some of their progeny were brought back to Chicago. While the percentage of the normal Chicago beetles that survived the winter in that locality averaged 79·46%, in the case of beetles which were bred for two generations in Arizona only 7·5% survived. Of the fourth Arizona generation only 2·25% survived the Chicago winter, and of the beetles bred in Arizona for eight generations none were able to hibernate in Chicago (Fig. 39). Acting on the suggestion that resistance to cold is due to the water content, experiments were made with the desiccation of Arizona and Chicago beetles. The results showed that the Chicago beetles lost their water content very rapidly, while the Arizona beetles were very resistant to desiccation. Thus, breeding under desert conditions even for a small number of consecutive generations brought about remarkably deep changes in the constitution of the beetles, rendering them much more resistant with regard to the dry environment, but weakening their ability to withstand low temperatures.

Babcock (1927*a*) experimented with the European corn-borer which produces one annual generation in New York, whereas in eastern Massachusetts the majority of individuals have two generations. When individuals from the one-generation area were transferred to the area where two generations are the rule, the original seasonal rhythm was maintained for several seasons.

The transportation of certain insects from North America to Australia for the biological control of the prickly pear (*Opuntia*) offered an opportunity for the study of the problem of acclimatisation. A Pyralid moth *Melitara junctolineella*, Hulst., which in Texas produces two generations annually was transferred from the winter in its native land to the Australian summer. During the first sixteen months in Australia three generations were produced, and further adjustment to the seasons tended to the stabilisation of a cycle of three annual generations (Hamlin, 1923). A Coreid bug (*Chelinidea* sp.) also proved able to adjust itself rapidly to reversed seasons (Alexander, 1925).

Cases of a species being unable to become acclimatised are also known. The Death's-head moth, *Acherontia atropos*, L., reproduces normally in Southern Europe, and adults are often captured very far north from the permanent area, but it is unable to survive there. Even when one generation is produced, the adults are infertile (Linde, 1897; Skell, 1928; Pabst, 1895). Similarly, the cabbage white butterfly, *Pieris brassicae*, L., is unable to become acclimatised either in Palestine, where the progeny is killed off by heat in summer (Bodenheimer, 1928), or in Northern Germany, where the hibernating pupae cannot withstand the frosts (Blunck, 1921).

It will thus be seen from the above that the important problem of acclimatisation has not yet received the attention it deserves.

(vi) *Geographical variation.*

In insects of wide geographical range the individuals from different parts of the range are often dissimilar in size, structure, and colour, the differences, however, not being sufficiently great to be considered of specific value. Moreover, the individuals from intermediate localities exhibit transitional characters between the extremes. This suggests that geographical variation may be regarded as an outward indication of the responses of the species towards local climatic conditions. The literature on geographical variation is very extensive, since in most systematic papers attention is paid to the geographical forms, but these papers are of little value for our purpose since they do not include attempts to correlate the variation with climatic factors. In so far as such attempts are made, they are based on purely theoretical considerations. The amount of exact work done on the climatic causes of geographical variation is very small.

A very good general survey of geographical variation in Lepidoptera, without a discussion of its climatic causes, has been published by K. Jordan (1905). He concludes that in most cases the differences between geographical forms are those of pattern and colour, but very often they are accompanied by anatomical differences in the genital apparatus, while in some cases the difference is only anatomical, the forms being similar in their external characters.

Alpatov (1927, 1929) studied biometrically the geographical variation of the honey-bee in Russia. More southerly bees proved to differ from northern ones by the smaller size of the body, relatively larger wings, longer tongue (Fig. 40), and the smaller wax-producing surface of the ventral segments. All these characters vary gradually as we move southwards.

Very extensive studies in the geographical colour-variation of the potato beetle, *Leptinotarsa decemlineata*, Say, were made by Tower (1906). This beetle exhibits melanistic tendencies in the Eastern United States, into which it has been relatively recently introduced. Generally speaking, the prevailing colour-forms in each climatically different area are distinct. When, however, individuals from various localities, were bred in Chicago, their progeny in the first or second generation resembled the Chicago form. Conversely, the progeny of Chicago insects, bred under conditions of temperature and humidity as observed in different parts of the area of distribution, showed variations typical for the respective areas. Other species of the same genus differ in this respect. *Leptinotarsa undecimlineata*, for example, varies very little geographically, and does not produce variations when experimented with.

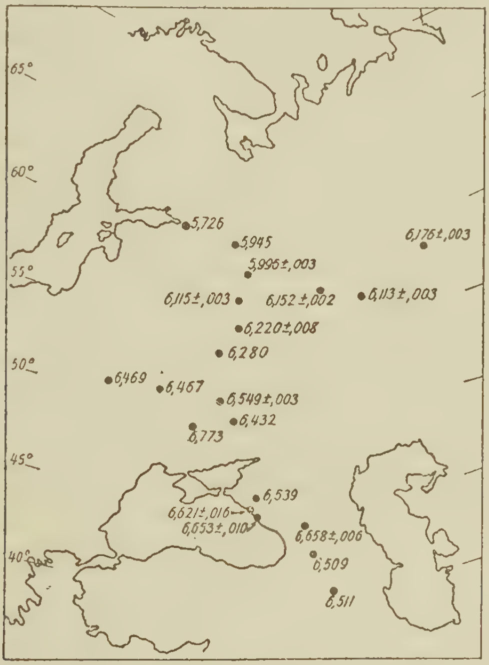

Fig. 40.—Geographical variation in the length of tongue of honey-bees in Russia. (After Alpatov, 1929.)

Shelford (1917) after very exhaustive studies on the distribution of tiger beetles (*Cicindela*) in North America found it impossible to correlate the variation in colour with any of the climatic factors. This is, however, due to the fact that the larval and pupal development of the beetles takes place in burrows in the soil, and the depth of the burrow varies in the same species according to the local climatic factors, thus counteracting the latter.

(There are a number of other papers on the climatic variation in colour; the following may be quoted merely as examples: Enteman, 1904; Fernald, 1926; Hudson, 1913; Walsingham, 1885; Manders, 1907; Pictet, 1904*a*, 1905*a*; Vogt, 1909–1911. Bachmetjew, 1907, gives a review of papers previous to his work.)

Geographical variation in size has been observed very often. Thus a number of Acrididae that spread from the Pacific Coast of Siberia into Europe, show a regular decrease in size from East to West. Bachmetjew (1909) studied the wing-expanse of *Aporia crataegi*, L., from 60 localities, and found that individuals from more northern localities generally have longer wings. Similar examples quoted by Titschak (1925) are in agreement with experimental data regarding the influence of temperature on the size of insects (see p. 38). Rudow (1900), however, reached the conclusion that in the case of Hymenoptera no general rule of this kind can be laid down.

Climatic variation in the absolute and relative size of different parts of the body has been mentioned already with reference to the honey-bee. Walker (1912) has published some interesting observations on the three species of dragonflies of the genus *Aeschna* which present a similar type of variation according to their distribution. In all of them, with an increase of the mean summer temperature, there is an increase in length and a decrease in depth of the third abdominal segment, and an increase in length of the female appendages.

Variation in the development of the organs of flight is often apparently climatic. For example, the small cricket, *Pteronemobius heydeni*, Fisch., is always brachypterous in Western Europe, but in the desert areas of Asia only occurs in the macropterous form. In the intermediate regions, in Palestine for instance, both forms are known (Chopard and Bellecroix, 1929).

A very interesting point has been raised by Stauder (1921), who has pointed out that species of butterflies which are feeble fliers in the northern areas, fly very strongly in the south. *Parnassius apollo*, L., in the Alps can be taken by hand, while in Italy its local form is a very strong flier and very difficult to catch. This suggests that the rate of activity of the same species may be affected considerably by the local climatic conditions. This is not surprising in view of what is known of the effects of temperature on the activity (see p. 87).

(*c*) **Ecological Distribution.**

Even species with a very wide geographical range do not occur in every locality within the range, but are restricted to more or less definite habitats. For example, one of the commonest and most abundant European grasshoppers *Chorthippus* (*Stauroderus*) *bicolor*, L., occurs in a variety of habitats, but not in marshes, while an allied species, *Ch. parallelus*, Zett., inhabits damp meadows. The two species may live within a few yards of each other, *i.e.* apparently under the same climatic conditions, if the latter are judged on the basis of the usual standard observations taken at a meteorological station, while in fact they are subjected to widely different conditions of temperature and humidity. In the study of insect ecology we must, therefore, pay special attention to the climate of the actual habitat of the insect, or to the *ecoclimate*, as I would suggest that the sum-total of meteorological factors within a habitat should be called. By a habitat is meant in this case a forest, a marsh, a sand-dune, etc. In many cases even this is not sufficiently exact. For example, the ecoclimate of a forest does not give an exact idea as to the conditions of temperature and moisture to which a larva boring inside a tree is subjected, since these conditions obviously are very different in a tree exposed to the sunlight from those of a similar tree standing in dense shade. A study of the *microclimate* of the actual medium where the insect lives becomes therefore inevitable if we want to understand in all their details the conditions to which it is subjected.

Thus, apart from the general climate of a country, or of a locality, ecoclimates and microclimates should be studied. This idea has already been expressed by several ecologists (Shelford, in particular), and formulated more definitely by Friedrichs (1930).

(i) *Ecoclimates.*

In spite of the obvious importance of the study of ecoclimates for the proper understanding of the actual conditions of existence, very little work has been done on the subject, though, of course, similar investigations have been carried out by plant ecologists. Their results are often equally valuable for entomologists.

Adams (1915) summarised the results of ecoclimatic observations in a forest and in a prairie, while Weese (1924) made similar studies in an elm-maple forest in Illinois for the specific purpose of evaluating the factors of the ecological distribution of animals, mainly insects.

With regard to air temperatures, the data summarised by Adams demonstrate clearly that the conditions of existence in a forest differ considerably from those in open country. Generally speaking, forests tend to reduce the fluctuation in the air temperature, as well as to lower the mean temperature. This influence is greater in summer than in winter. The temperature of the soil in forests is higher in winter but lower in summer than in the open. This is a factor of extreme importance for a large number of insects.

The light conditions in a forest, again, are of importance for the ecological distribution of insects. That some insects are guided in their distribution by the intensity of light is evidenced by the experiments described by Shelford (1929). Insects from a given habitat were put into a dark box, of which the lid was made in three sections, one dark, one medium, one wholly transparent. The percentage under each section was counted. In one of these experiments, 54% of the flies taken from amongst herbs in a wood collected in the dark section, 40% in the medium and only 6% in the light section, whereas, in the case of tree-hoppers taken also from herbs, but on a road, the percentage in the light section was 50%, and 25% collected in the medium and the dark section respectively (see also O. Park, 1929).

Since forests present a great variety of types, it is natural to expect a corresponding diversity in their ecoclimates and, consequently, in their population. The injury caused by *Pissodes pini*, Peck., is much less in mixed forests where hardwoods shade the pine (there being no injury at all in the shade of oaks or maples) than where open pure stands of white pine grow in full sunlight and are attacked most seriously (Graham, 1926; see also De Gryse, 1929; Craighead, 1919; Safro, 1929). Wladimirsky (1926) made a quantitative study of the entire population of plants of *Urtica* growing respectively in the open and in the shade. The results he obtained are illustrated by Table XXXIII and by the diagram given in Fig. 41.

TABLE XXXIII.

Population of Plants (*Urtica*) in the Open and in the Shade. (After Wladimirsky.)

	Acarina.	Aphididae.	Psyllidae.	Collembola.	Thysanoptera.	Predators.	Others.
	%	%	%	%	%	%	%
Open .	4·2	53·2	30·3	0·6	7·3	2·2	2·2
Shade .	22·4	1·4	19·6	46·0	1·1	0·7	8·8

The total population was smaller in the shade (163 insects per plant) than in the open (664 insects per plant). When calculated to 100 sq. cm. of the leaf surface the population in the open was 21 times that in the shade.

The importance of ecoclimatic conditions in the distribution of tsetse flies in Africa is exceptionally great, the flies depending closely on a certain degree of humidity and the absence of direct sunlight which is injurious to them (Roubaud, 1920; Fiske, 1920; Swynnerton, 1921).

Ecoclimates of different habitats in a desert were studied by Buxton (1924), Williams (1923, 1924, 1924*a*) and by Chapman, Mickel, Parker, Miller and Kelly (1926). The temperature range of a black bulb thermometer in the open desert in Egypt, according to Williams, is 38° greater than the range in a meteorological screen, that of the white bulb 15° greater and the evaporation 1·4 times that in the screen. These figures indicate that standard meteorological observations have a very remote relation to the actual conditions of existence of insects even in the immediate vicinity of a meteorological station.

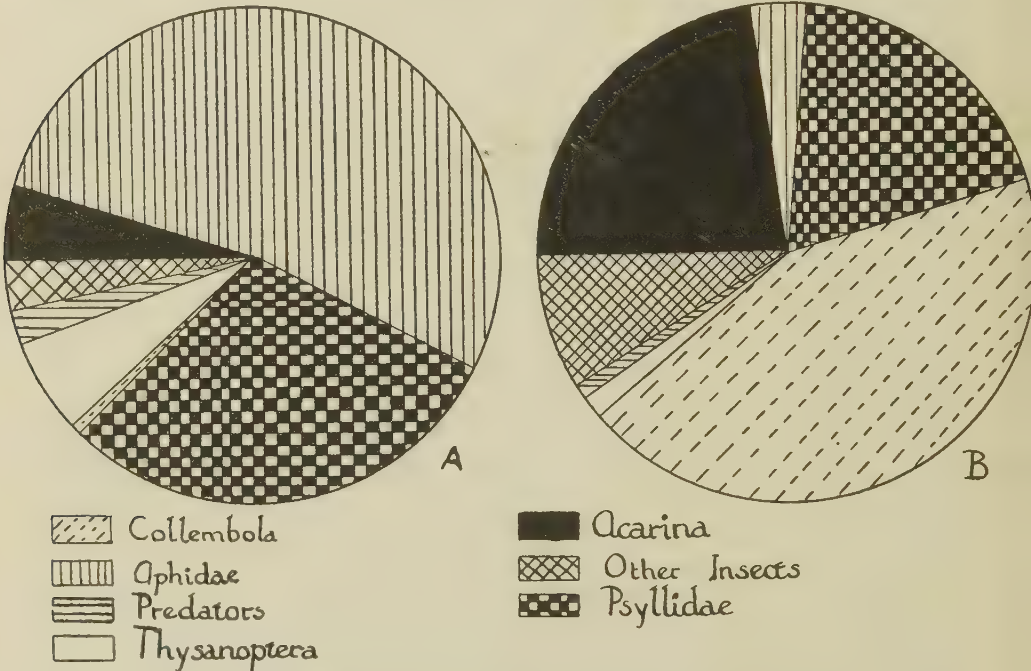

Fig. 41.—The ratio of different groups of the population of *Urtica* in the sun (A) and in the shade (B). (Re-drawn after Wladimirsky, 1926.)

The ecoclimates of cultivated lands present a special interest to economic entomologists. The lack of work in this direction is deplorable. A very instructive example of the necessity of taking the ecoclimatic conditions of crops into consideration is offered by the data on the distribution of the Mexican bean beetle, *Epilachna corrupta*, Muls. This beetle is a serious pest in the parts of Mexico which have a hot and very damp climate, on one hand, and in the Western United States, with their semi-desert climate, on the other. Graf (1925), who attempted to study the factors of the distribution of this beetle on the basis of the standard data of meteorological stations, arrived at the conclusion that it is not the climatic factors which condition the distribution of the beetle. Sweetman (1929), however, pointed out that in arid localities the infestation is largely confined to the irrigated lands, the ecoclimate of which, as far as humidity is concerned, naturally differs very considerably from the general climate of the area. Again, Janisch (1930) pointed out the importance of irrigation for the existence of *Prodenia litura*, F., in Egypt. Ohlendorf (1926) has published some interesting figures showing that irrigation may have an opposite effect, since in unirrigated fields in Mexico 12·8% of the hibernating larvae of the pink boll worm produced moths, while none of the larvae in the irrigated fields survived the winter. The relative percentage of survival in this case had no relation to the general climate. Similar data were published by Wardle (1927) on the influence of irrigation on thrips on cotton.

A detailed examination of ecoclimatic conditions, as governed by vegetation, relief of the ground, etc., is given in a recent book by R. Geiger (1927).

(ii) *Microclimates.*

Ecoclimatic observations represent the conditions of existence of insects more correctly than the standard climatic data, but they cannot be considered as sufficiently exact. Indeed, the actual, *i.e.* the microclimatic, conditions often bear only a very remote relation to the general conditions in the habitat.

To begin with, the ecoclimate of a habitat with a thick layer of vegetation, *e.g.* of a forest, shows great vertical variation. The relative humidity of the air is greatest at the ground level, and decreases as the height increases. The temperature gradient has an exactly opposite direction in summer, while in winter the highest temperatures are in the soil, and the temperature decreases upwards. The gradient of the evaporative power of the air is very striking. An insect passing from the surface of the soil to the top of a tree would enter a region of three times the average evaporative power. The ratio of light intensity between the ground stratum and the shrub stratum may be as high as one to three or one to four (Weese, 1924; see also Adams, 1915). How this difference affects the distribution of insects is illustrated by the following table showing the number of species from the different strata of a pine forest on sand (see Table XXXIV).

TABLE XXXIV.

THE NUMBER OF SPECIES OF INSECTS FROM DIFFERENT STRATA OF A PINE FOREST.
(After Sanders and Shelford.)

Stratum.	Number of species.	Average temperature.	Range of temperatures.
Ground	10	25·4°	25°
Herbs	35	21·2	16
Shrubs	38	21·0	8
Trees	11	21·2	11

The above table shows that the shrub level, where changes in the temperature are the least, is the most thickly inhabited.

Townsend (1928) has recorded a very interesting observation on the fly *Psilophus sipho*, Say, which in a wood migrated from the ground level to the tree tops as soon as the grass was mown. Atmometer records showed that, before mowing, the lowest rate of evaporation was near the ground and that after it the conditions became reversed, so that the flies evidently migrated to the stratum having the lowest evaporation rate.

Apart from the vertical strata, there are, for a number of reasons, great differences between the microclimates of situations at the same level. The relative density of foliage of two trees standing side by side would greatly affect the microclimatic conditions under them, because of the differences in radiation and in ventilation. The microclimatic conditions on the two sides of a tree trunk differ considerably, *e.g.* the temperature on the side facing south may be 15–20° higher than that on the north side. This causes a difference of 26–28 days in the emergence of the Oriental peach-moth emerging from pupae on the north and south sides of the tree respectively (Peterson and Haeussler, 1928).

It is well known that some insects always keep on the under-surface of leaves, while others feed on their upper surfaces. The microclimatic conditions to which such insects are subjected may be expected to differ considerably, although no observations have been made on this point. Chaine (1912) has recorded observations on a leaf-mining Cecidomyiid, *Monarthropalpus buxi*, Lab., the larvae of which were killed in hot weather in leaves exposed to the sun, but not in those in the shade.

Highly specialised microclimatic conditions are experienced by insects that live inside plants. With regard to wood-boring insects, some most interesting results have been published by Graham (1921, 1922, 1924, 1925), who studied very carefully the microclimates in logs infested with insects. The temperature within a log does not depend entirely on the air temperature, since the absorption of radiant heat in the case of direct sunlight causes the temperature in the log to rise to 60° when the air temperature is 40°. The temperature conditions are of course not the same in differently exposed parts of the log, and this affects the distribution of insects, the various species having different requirements. Table XXXV, which shows the distribution within a pine log of a highly thermophilous species, *Chrysobothris dentipes*, Germ., and of *Ips pini*, Say, which is less so, may serve as an illustration (see also Patterson, 1930).

TABLE XXXV.

NUMBER OF INSECTS PER UNIT AREA IN DIFFERENT PARTS OF A LOG. (After Graham.)

	Upper side.					Under side.				
	Degree of shade.					Degree of shade.				
	0	⅓	½	¾	Full	0	⅓	½	¾	Full
Ips pini . . .	73·4	69·4	164·2	125·9	41·5	40·0	16·5	31·4	35·8	44·1
Chrysobothris dentipes .	12·0	1·0	0·3	0	0	0	0	0	0	0

Moisture conditions inside logs have also been found to vary considerably, partly in correlation with meteorological conditions. The distribution of larvae of *Asemum* and *Monochamus* have been shown to be dependent on this microclimatic factor.

The temperature and moisture within logs have an important influence not only on the distribution, but also on the rate of development of insects. Indeed, *Monochamus scutellatus*, Say, in the sun completes its development in one year, whereas in shade it may require three full years (Graham, 1925). Thus, within the same log there exists a range of conditions such as one would expect only in widely distant geographical areas with entirely different climates.

Microclimatic conditions to which insects living inside herbaceous plants are subjected have never been studied with the exception of cotton bolls. Kirkpatrick (1923) found that the temperature within an open boll tends to be lower than the shade temperature during the day, and that at night the minimum within the boll appears to be above the minimum air temperature. On the whole, therefore, the microclimatic conditions within a cotton boll are very different even from the ecoclimate of the cotton field, to say nothing of the data recorded in a meteorological shed.

The microclimates of hibernation shelters present a great practical interest, but again, no research has been done in this direction. There is, however, some indirect evidence as to the value of winter protection. Grevillius (1905) recorded that the larvae of *Nygmia phaeorrhoea*, Don., in their winter nests can withstand a temperature of —31° for 24 hours, while larvae taken out of nests are killed by the temperature of —14° in a few hours. Kulagin (1897) recorded that the eggs of *Porthetria dispar*, L., are not killed by a temperature of —50° if the cluster is covered with wool, as it normally is, but when the wool is removed the eggs cannot even survive a temperature of —19° (see also Reiff, 1910). According to Weiss (1914) cocoons of Lepidoptera protect the pupae from sudden changes in the temperature. Urech (1890) made some observations on the protective value of cocoons of *Malacosoma neustria*, L., against desiccation. A pupa taken out of a cocoon lost up to 9·42% of its weight in 5 days, whereas a pupa in the cocoon lost only 3·5%. Hinds, Yothers and Hunter (1909) studied the conditions of survival of the cotton-boll weevil during hibernation, and found that the weevils hibernating in bolls were subject to greater mortality than those hibernating in other shelters.

Insects hibernating on the surface of the soil (under leaves, etc.) or in the soil, may be subjected to very different degrees of cold according to the absence or thickness of the snow cover, which, owing to snowdrifts, may vary greatly within a few yards. The subject of the protective value of snow is discussed elsewhere (see p. 140).

A special case of microclimatic conditions is offered by caves and burrows. Fleas living on wild rodents in their burrows are subjected to a microclimate which is very different from the ecoclimate outside the burrow. The temperature in the burrow is higher in winter and lower in summer, and the humidity is always greater than above ground (Ingram, 1927). Williams (1923, 1924, 1924*a*) investigated the microclimate of some, not very deep, caves in the Egyptian desert, and found that even at a depth of 20 metres there was practically no annual variation in the temperature, while the temperature on the surface of the sand outside varied from 5° to 60°. The humidity was also very constant, and on the whole, the microclimatic conditions in a cave were found to be extremely dissimilar to those outside. This means that an insect living in a desert, but which, as many do, hides during the day in a cave and comes out only at night, is never exposed to the desert climate with its extreme factors.

The microclimatic conditions of large caves are very peculiar and are characterised mainly by an almost constant temperature, exceedingly high humidity and the absence of air movement. High humidity is considered by several authors to be the principal factor in the life of cavernicolous insects (Jeannel, 1926; Rabaud, 1911; Depoll, 1920; Fagniez, 1907). Jeannel pointed out that many cave beetles are extremely sensitive to the slightest movements of air, such as cannot be registered by the most exact anemometers

The microclimatic conditions in the soil, which bear only a very distant relation to the ecoclimate above its surface, are very important in the life of a great percentage of insects. The soil temperature, for example, is much less variable than the air temperature, the annual range at one foot below the surface being only half that of the air. Moreover, the soil temperature depends less on the air temperature than on radiation and conduction of heat. The absorption of radiant heat and its conduction depend on many factors which vary within a short space, viz. the density of vegetation, exposure of the slope, chemical and physical properties of the soil, etc. Again, the moisture conditions in the soil, while dependent partly on the precipitation and the evaporation, cannot be deduced from observations on the latter, and should be studied separately. For insects that live in the soil during at least one stage in their development, the temperature and humidity of soil are factors of outstanding importance. For example, Central Russia is geographically outside the range of the continuous distribution of the Migratory Locust, *Locusta migratoria*, L., but it occurs in that region in some isolated spots on sandy soil, which is the warmest and the driest found there. In this kind of soil the eggs of the locust can hibernate and develop safely (Predtetchenskiĭ, 1928). On the subject of the microclimate of soils see also Cameron, 1913; Hamilton, 1917; Handschin, 1929; Holmquist, 1928; McColloch and Hayes, 1922, 1923; McColloch, Hayes and Bryson, 1928; Parker, 1915, 1929, 1930; Prinz, 1928; Shelford, 1911, 1912; Tower, 1906.

The microclimatic conditions to which the insects parasitic on other animals are subjected are highly peculiar. The clothes-louse, *Pediculus vestimenti*, L., cannot survive for more than three days in the ordinary room temperature, *i.e.* 16–22°, and in experiments on their preferendum they collected within the range of 24–32° (Martini, 1917). They have to rely, therefore, on the warmth from the body of their host, while their humidity conditions have also scarcely any relation to the air humidity outside the clothes. In other words, the lice live in a special microclimate, and this applies also to other parasites of warm-blooded animals.

Even with regard to blood-sucking insects which come into contact with the host only when feeding, the microclimate on the surface of the host is of importance. Thus, the mosquito, *Anopheles maculipennis*, Mg., is inactive at temperatures below 6·5°, but if brought into contact with a hand, it would suck blood when the air temperature was as low as 3·5°, for the air immediately surrounding the hand may then be at 13·2° (S. Shtcherbakov, 1927).

Finally, we have to consider briefly the microclimates within the nests of social insects. Reaumur (1740) discovered nearly two hundred years ago that the temperature inside a beehive is in winter much higher than that of the outer air, and observed that the bees can raise the temperature by wing movements. Since his time, the problem of the temperature conditions in beehives has been investigated thoroughly by a number of authors. It has been found that a fall in the outside temperature induces the bees to form a dense cluster. With a further fall in the temperature (below about 13°), they become restless and begin to move. As a result of these movements the temperature in the cluster rises to about 25–30°, at which point these movements begin to slow down. The temperature inside the cluster then begins to sink until it reaches about 13°. The fluctuations in the external temperature are reproduced faithfully by the corresponding, but inverse, fluctuations inside the clusters, *i.e.* when the air temperature falls very low, that of the cluster becomes very high owing to the more energetic movements of the bees (see Fig. 42). In this way the microclimate within the hive is kept practically independent of the climatic conditions (see Armbruster, 1922–1925; Bruman and Liechti, 1929; Brünnich, 1925; Buddenbrock, 1928; Dubost, 1880; Gates, 1914; Hess, 1926; Himmer, 1924–1927; Hochegger, 1925; Kulagin, 1898; Milner and Demuth, 1921; Molin, 1880; Newport, 1837; Phillips and Demuth, 1914; Schönfeld, 1866; H. Wilson and Milum, 1927; Zander, 1917).

Other social Hymenoptera are also able to regulate the temperature inside their nests, though to a lesser degree than honey-bees. Janet (1895) observed that the difference between the air temperature and that in the nest of *Vespa crabro*, L., ranged from 2·5° to 15°. For *V. vulgaris*, L., the difference was 2–20°. Himmer (1925, 1927*a*) and Steiner (1930) studied the regulation of the temperature inside the nests of *Polistes gallica*, L. When the temperature in the nest rises, owing to the absorption of the radiant heat, to about 31–35°, the wasps begin to fan their wings and thus lower the temperature. At about 34–37° another method of lowering the temperature comes into operation, viz. the wasps begin to bring water into the nest, and its evaporation, aided by fanning, lowers the temperature.

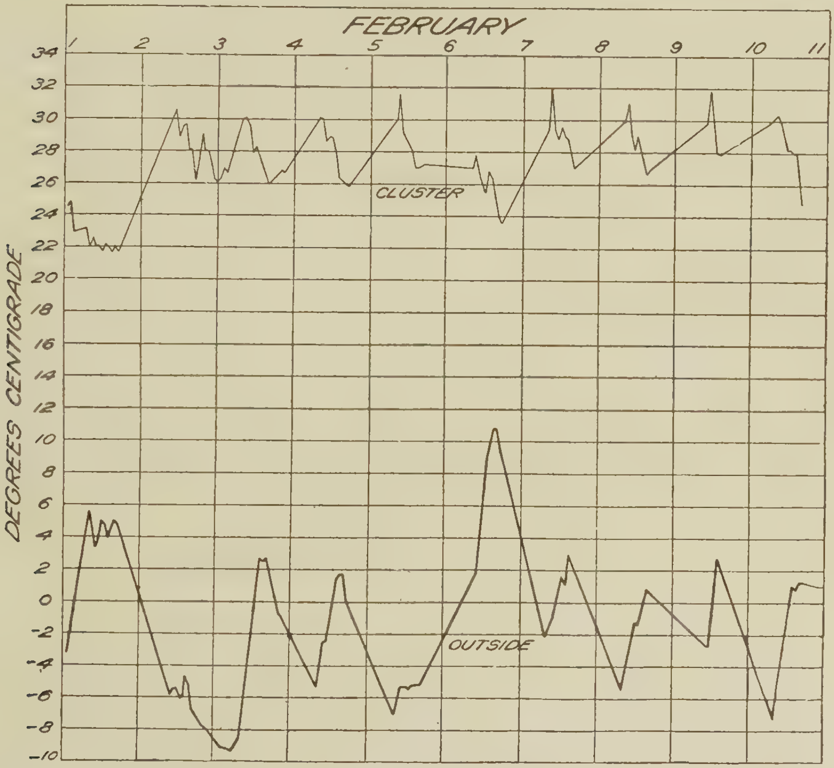

Fig. 42.—Curves showing the relation of the temperature in the centre of a bee cluster to the outer temperature. (After Gates, 1914.)

The temperature in nests of bumble-bees (*Bombus*) has been studied by Newport (1837).

Ant-nests present a microclimate of their own. This has been noticed already by Juch (1800) and Ormerod (1879*a*), while recently Holmquist (1928), Wellenstein (1928) and Steiner (1924, 1925, 1929) carried out detailed investigations on the subject. A zone of practically constant temperatures of about 23–29° was found at the depth of 15–50 cm. in the nests of *Formica rufa*, var. *rufopratensis*, For. This temperature is about 10° above the soil temperature at the corresponding depth, and coincides with the optimum breeding temperature. The regulation of the temperature in the ant-heap is based mainly on the insolation of the cupola, and on the opening and closing by ants of exits at the sides either exposed to the sun, or away from it.

A temperature considerably higher than that of the air occurs in the segregations of some other insects. Caterpillars of the wax-moth, *Galleria melonella*, L., live in dense colonies in honeycombs, and the temperature inside the colony may exceed that of the outside air by 17–22·7°. The difference may be due partly to fermentation and partly to the temperature of the caterpillars (Girard, 1865; Hase, 1926). Aggregations of other insects for hibernation may also possibly have a microclimatic meaning, but so far this has not been investigated.

The microclimates of the environment in which household insects live are, of course, widely different from the climate of the country, however. No work has been done on this subject. An interesting case is presented by the house-cricket, *Gryllus domesticus*, L. This is an insect of Palaearctic deserts (Sahara, Persia), which has been carried by man into many countries, where it lives in the dry and warm parts of houses. Both in England (Austen, 1921) and in France (Chopard, 1928) the cricket found its way with the kitchen refuse into large refuse dumps near towns, where there is continuous warmth owing to self-combustion. This semi-artificial microclimate enables the cricket to live out of doors in very unfavourable climates.

VIII. EFFECT OF CLIMATE ON ABUNDANCE.

(*a*) Biotic Potential and the Coefficient of Destruction.

The great fertility of insects in general is well known. There are very few insect species which, judging by the number of eggs laid, may be expected to increase less than tenfold in one generation, while in many cases the theoretical ratio of the increase may be counted in hundreds and thousands. The number of generations in a year may also be very considerable. These theoretical calculations lead to the inevitable conclusion that practically any insect should be able to multiply its numbers within a short time to limits verging on absurdity, and the earth's surface appears too small for the theoretical progeny of a single pair. Nothing of this kind happens in nature, and we must conclude, therefore, that there are forces at work which counteract the natural tendency of each species to multiply indefinitely. These forces must amount to a continuous elimination of a certain percentage of progeny. A simple theoretical calculation shows that this percentage must be very high in order to keep the numbers at the average level. Thus, in the case of an insect laying 100 eggs, as many as 98% of the progeny must be regularly eliminated to prevent the numbers increasing, *i.e.* only two individuals of the offsprings of each pair should reach maturity. In the more prolific species of insects the percentage of survival must be expressed in small fractions. This correlation between the potential increase of an insect (or its *biotic potential*, according to the terminology introduced by Chapman, 1926) and the controlling factors has been expressed by Bremer (unpublished; see Blunck, 1929) by a formula for the normal *coefficient of destruction*, representing the percentage of progeny which must normally be eliminated in order to keep the population at the same level. Bremer's formula is—

$$q_c = 1 - \frac{b^c}{a^c}$$

where q is the coefficient of destruction, a the number of progeny of a female, b the ratio of females (*e.g.* when there are 50% of females, $b = 2$) and c the number of generations a year. In the case of *Pegomyia hyoscyami*, Pz., a equals 50, b equals 2, c equals 3. The normal coefficient of destruction would, therefore, be 96% for one generation and 99·99% for all three generations of one year. In other words, the survival of only 0·01% of individuals produced during the year is sufficient to keep the number of flies at the same level. The coefficients of destruction of other pests are also very high, *e.g.* for *Melolontha melolontha*, L. (with 24 eggs per female and one generation in four years) it is 23% in a year, and 92% in a generation; for *Meligethes aeneus*, L. (400 eggs and one annual generation), 99·5%; for *Euxoa segetum*, Schiff. (1500 eggs, one generation), 99·9%, etc.

The coefficient of destruction is, therefore, enormously high, even in the case of an insect like *Melolontha*, which cannot be considered either very fertile, or as developing rapidly. This being so, one must be very careful not to overestimate the controlling value of any individual factor. These factors include the meteorological conditions unfavourable for life, development and reproduction, as well as predators and parasites, diseases and shortage, or unsuitable quality, of food. It is remarkable that most authors of text-books consider mainly the food, parasite and disease factors, either ignoring the climatic influences, or only incidentally mentioning them. The present section is devoted to the evidence on the controlling value of the climatic factors.

(*b*) **Temperature as a Controlling Factor.**

(i) *Direct injury by high and medium temperatures.*

High air temperature in nature may often reach the upper fatal limit (see p. 17) of an insect. Cases in which the body temperature of an insect rises above the fatal limit owing to the absorption of radiant heat are still more frequent. Several authors have made sufficiently exact observations on the effects of heat on the cotton-boll weevil under natural conditions (Pierce, 1926; Hinds, 1907; Sanderson, 1907). These observations show that as many as 54·7–58·5% of the insects in bolls and squares may be killed by radiant heat. Stellwaag (1925, 1927, 1928, 1929), Feytaud (1919, 1923) and Chauvigné (1920) consider that high temperatures are a very important controlling factor in the case of the vine moths (*Clysia ambiguella* and *Polychrosis botrana*). According to the data of these authors up to 50% of the eggs may be killed by heat, and newly hatched caterpillars may be killed by direct sunlight. Dewitz (1906, 1906*a*, 1912) pointed out that even moderately high temperatures, *e.g.* 40°, which are not immediately fatal, are definitely injurious, and Janisch (1930) insisted that any deviation from the optimum temperature, however slight, has its after effects, although he has not produced sufficient evidence to support his views. Chaine (1912, 1919) records definite instances of the fatal effects of heat-waves on insects, *e.g.* rose Aphids, *Aphis rosae*, L., were killed off at Bordeaux on July 9th, 1911, by a sudden rise in the temperature to 37°. Swain and Duggan (1928) consider that normally up to 50% of the young stages of the black scale *Saissetia oleae*, Bern., are killed off by heat in summer. One abnormally hot week in June, with maximum temperatures 37–47°, resulted in an effective control of the scale.

In many cases heat acts fatally, or injuriously, in connection with low humidity. This combination is discussed later (see p. 148).

(ii) *Effect of high temperature on fertility.*

Experimental data on this subject, reviewed elsewhere (see p. 48) suggest that the effects of heat and of abnormal temperatures generally on the fertility of insects may be one of the most important factors controlling their abundance. Unfortunately, observations on this point made under field conditions cannot be expected to be conclusive or exact. The best known cases refer to the infertility of certain Lepidoptera caused by excessively hot weather, but this conclusion has been disputed (see p. 48).

A peculiar case of a moderate temperature causing the elimination of a considerable percentage of progeny has been observed in the Colorado potato beetle, which on cool days begins to feed on the eggs of its own species, laid on leaves. Sometimes as much as 74% of the egg-masses may be partly, or wholly, eaten (Gibson, Gorham, Hudson and Flock, 1925).

The rate of reproduction is also affected by temperature in a fundamental way, as has been shown in another section (see pp. 49, 92).

(iii) *Winter mortality and effects of low temperature generally.*

The mortality of insects caused by winter colds is probably the main factor controlling the abundance of most insects in temperate latitudes. Of course, the controlling value of winter mortality is very unequal in the case of different insects. It depends, first, on the stage in which the insect passes the winter. Bremer (1928*a*) divides the more common European pests into two groups, as follows :—

1. Mass outbreaks dependent on the winter conditions.
    - *Euxoa segetum*, L., hibernates as larva.
    - *Operophtera brumata*, L., hibernates as adult.
    - *Eriosoma lanigera*, Schiff., ,, ,, adult.
    - *Pyrausta nubilalis*, Hübn., ,, ,, larva.
2. Mass outbreaks not dependent on the winter conditions.
    - *Tortix viridana*, L., hibernates as egg.
    - *Pegomyia hyoscyami*, Pz., hibernates as pupa.
    - *Clysia ambiguella*, Hübn., ,, ,, pupa.
    - *Polychrosis botrana*, Schiff., ,, ,, pupa.

These lists demonstrate that insects hibernating in an inactive stage are, generally speaking, less susceptible to the winter cold.

Another factor determining the effects of winter cold is the weather during the late autumn. We have seen that the resistance of an individual insect to cold may be greatly increased by a hardening, which is accomplished either by the gradual lowering of the temperature, or by the reduction of the free water in the organism. Thus, a mild and wet autumn followed by sudden frosts is more injurious than a dry autumn with a gradual decrease in the temperature. Moreover, even the weather conditions during the preceding summer may influence the winter mortality. If the summer is abnormally hot, or abnormally cold, there may be a partial displacement of the normal sequence of generations, or of stages, with the result that the stages not normally exposed to winter conditions will be so exposed. This applies particularly to species that do not have a fixed annual cycle (see p. 105), and which hibernate in an active stage.

Mild and unsettled conditions during the winter are more injurious to hibernating insects than are continuous frosts. The abundance of insects after exceptionally severe winters has been often noticed in the literature (*e.g.* by Barrett, 1882; Jungner, 1904; Feytaud, 1919*a*). Hase (1927) from his experiments on the eggs of the flour moth, *Ephestia kuehniella*, Zell., concluded that after a cold winter the hibernating eggs of insects only hatch out when the warm weather definitely sets in, while in a mild winter they may hatch during warm spells, or even during cold intervals (owing to the delayed response to heat, as was observed in his experiments). Similarly, Handschin (1929) points out that insects hibernating in the soil may be induced during warm spells to move to the upper layers, where they are easily killed by subsequent frosts.

These are, of course, partly theoretical considerations, on the basis of which it would be unsafe to generalise. However, the idea that mild winters are favourable to insects appears very doubtful.

The percentage which winter mortality can attain, even in an average winter, is often very high. In the case of the eggs of the gipsy moth, up to 70% of the egg-masses may be killed by frosts (Summers, 1922). The winter mortality of the larvae of the European corn-borer in the United States may reach 60% (Barber, 1924, 1926). Kaufmann (1925) records that the percentage of the females of the beetle *Psylliodes chrysocephala*, L., killed by frosts is higher than that of the males, which seem to be less susceptible to cold. This observation has an important bearing on the problem of fertility as affected by winter conditions. (Other data on mortality during an average winter can be found in most economic papers; the following may be quoted as examples: Chittenden, 1900; Hinds, Yothers and Hunter, 1909; Webster, 1915; Zirnitz, 1926; Newell and Dogherty, 1909; W. Yothers, 1917; Beal, 1927.)

It must be stressed that for some species the winter cold is apparently of little importance. Feytaud (1923) suggests that this is the case with the vine moths (*Clysia* and *Polychrosis*), which are controlled mainly by summer conditions.

Observations on the effects of abnormally severe winters are of interest in the study of the fluctuations in the numbers of insects. Several authors (Catchings and Whitcomb, 1924; Marlatt, 1899; W. Scott, 1899; Spuler, 1920; Yothers, 1917) have recorded mortality as high as 100% in scale insects (Coccidae), as a result of exceptional frosts. During the severe winter of 1919, all codling-moth larvae were killed in localities in the State of Washington, in which the minimum temperature reached —38·5° (Newcomer, 1920).

The kind of shelter under which an insect hibernates is naturally very important for the percentage of survival. Barber (1924) found that the mortality of the hibernating larvae of the European corn-borer in New England varied greatly according to the plant in which they hibernated, as is shown in Table XXXVI.

TABLE XXXVI.

The Percentage of Winter Mortality of European Corn-borer Larvae in Different Plants. (After Barber.)

Pigweed (*Amaranthus retroflexus*, L.)	14–21
Barnyard grass (*Echinochloa crusgalli*, L.)	9·6–10·9
Polygonum	0–4
Hemp	4·5
Maize, top foot of stalks	51–60
do. middle section of stalks	41–43
do. bottom foot of stalks	19–26·5

The table demonstrates great differences in the winter microclimates inside various plants.

The data in the table referring to maize show the value of the protection offered by the snow-cover, the mortality being much lower near the ground, *i.e.* amongst the larvae in the parts of the stalk covered by snow. Hartzell (1929) made a special study of the relation of snow-cover to the survival of the cocoons of the grape berry moth, *Polychrosis viteana*, Clem. During an ordinary year, the most heavily infested places are where snow drifts normally occur in the vineyard during the winter, cocoons in the places covered with thinner layers of snow being killed off by frosts. Sacharov (1928, 1930) presents more exact observations on *Euxoa segetum* in the Saratov district, S.E. Russia. During the winter 1923–1924 the snow cover was as thick as 29·6 cm., and the soil temperature at a depth of 25 cm. did not fall below —5·5°. An outbreak of *Euxoa* occurred in the following spring. During the next winter the snowfall for a single month did not exceed 4·5 cm., the soil temperature at 25 cm. dropped to —12°, and there was no outbreak. Similar observations on the protective value of snow have been made by Summers (1922); Criddle (1917); Jacobi (1889).

The protection from winter cold offered by cocoons, etc., has been discussed elsewhere (see p. 133).

Spells of cold weather during the summer months cannot be without their influence on insect life, but there are no sufficiently exact data on this point. Judging from the information contained in the first section of this paper, low temperature, if not necessarily causing immediate mortality, affects the rate of development and all functions including reproduction in a most fundamental way. The effects on the earliest stages must be particularly important. Observations on this point are, unfortunately, not easy to arrange under natural conditions.

(iv) *Favourable effects of temperature.*

The general effects of favourable temperature on the rate of development, activity and reproduction have been discussed in the first section of this paper. It is proposed here only to quote a few examples, which suggest that favourable temperatures are often a direct cause of mass outbreaks of insects.

A plus deviation from the mean temperature of summer months is, according to Hesselink (1928), a condition likely to lead to an abnormal increase in the numbers of *Panolis flammea*, Schiff., in Holland. For a severe outbreak to occur two hot summers must follow each other in succession. Simmons and Ellington (1925), on the basis of a study of the climate of Philadelphia for 28 years, concluded that the principal factor influencing the outbreaks of the angoumois grain moth, *Sitotroga, cerealella*, Ol., is a favourable temperature from June to October. As regards cockchafers (*Melolontha*), Zweigelt (1928*a*) in his exhaustive monograph reached the conclusion that mass outbreaks of this pest are possible only in areas in which the mean temperature from May to October reaches at least 12·5°. Kleine (1923, 1926) insisted on the importance of a sufficient accumulation of favourable temperatures for the outbreaks of *Pegomyia hyoscyami* and *Chlorops taeniopus*.

The normal annual course of temperature (*i.e.* the one that deviates least from the average) is, generally speaking, more favourable to an increase in insect numbers, because it coincides best with the inherited rhythm of development. For some insects, however, abnormal seasons are more favourable. Wilhelmi (1920*a*); Wilhelmi and Saling (1928); Knoch (1921, 1923) put forward a theory of mass outbreaks of SIMULIIDAE in Europe according to which in a normal spring, with a gradual rise in the temperature, SIMULIIDAE hatch gradually and the cattle become immunised against their poison. Sudden rises in the temperature cause a mass hatching of the gnats, which attack non-immune cattle and cause an epizootic. The influence of heat-waves on the increase in numbers of certain, normally rare, species of insect has often been noticed by collectors (Stauder, 1928).

The relation of temperature to insect outbreaks in tropical countries is insufficiently known. Corbett and Dover (1928) believed that in Malaya, where the annual temperature is remarkably constant, it may be considered negligible as a factor in producing insect outbreaks.

(*c*) **Precipitation.**

(i) *Excessive precipitation.*

It is not possible to estimate the effects of abundant precipitation on the numbers of insects by direct observation, but the controlling value of this factor can be judged from the fact that for a number of insects the reverse condition, *i.e.* a deficient rainfall, or a drought, are definitely favourable and result in mass outbreaks.

A classical example of this kind is offered by the bark-beetles. Excessive rainfall during the flight of the adults checks their activities and reduces their progeny, while adults making burrows, as well as eggs and larvae, are liable to be drowned in the sap, which is more abundant when the moisture content of the soil is high. This statement is not based solely on theoretical considerations, since the development of bark-beetles in a tree can be checked to a considerable extent by supplying water to its roots, or by defoliating it and thus recording the loss of water through transpiration. Fig. 43 illustrates the connection between rainfall deficiency and an outbreak of bark-beetles. (See papers by Blackmann, 1924; Craighead, 1925, 1928; Felt, 1914; Middleton, 1928, 1929; St. George, 1926, 1929.)

Several authors have found that outbreaks of various species of cutworm (larvae of NOCTUIDAE) are favoured by deficient precipitation. Cook (1926, 1928*b*), Seamans (1923) and De Gryse (1929) recorded that outbreaks of the pale Western cutworm *Porosagrotis orthogonia*, Morr., depend on the total rainfall from May to August of the preceding year being less than 4 inches. Usually two favourable years in succession are required to produce an outbreak (in this case the controlling action of precipitation may be indirect, see p. 153). With regard to the European species of cutworm, *Euxoa segetum*, Schiff., the data are contradictory. Azov (1929), who studied this insect in the North-Dvina province of Russia, stated that the main controlling factor is the rainfall in May. If it is under 40 mm. the pest increases, but when the rainfall exceeds 80 mm. its numbers are reduced to a minimum. Shtchelkanovtzeff (1926*a*), on the contrary, concluded, from an analysis of the occurrence of *E. segetum* in the Voronezh province for a period of 50 years, that the outbreaks of this species are favoured by high precipitation. Eleven out of thirteen outbreaks which occurred during that period took place in years in which at least one of the summer months had more than 50 mm. of rain. In dry years the insect disappears as a pest. This contradiction may be due to the difference between the normal climates of the two areas.

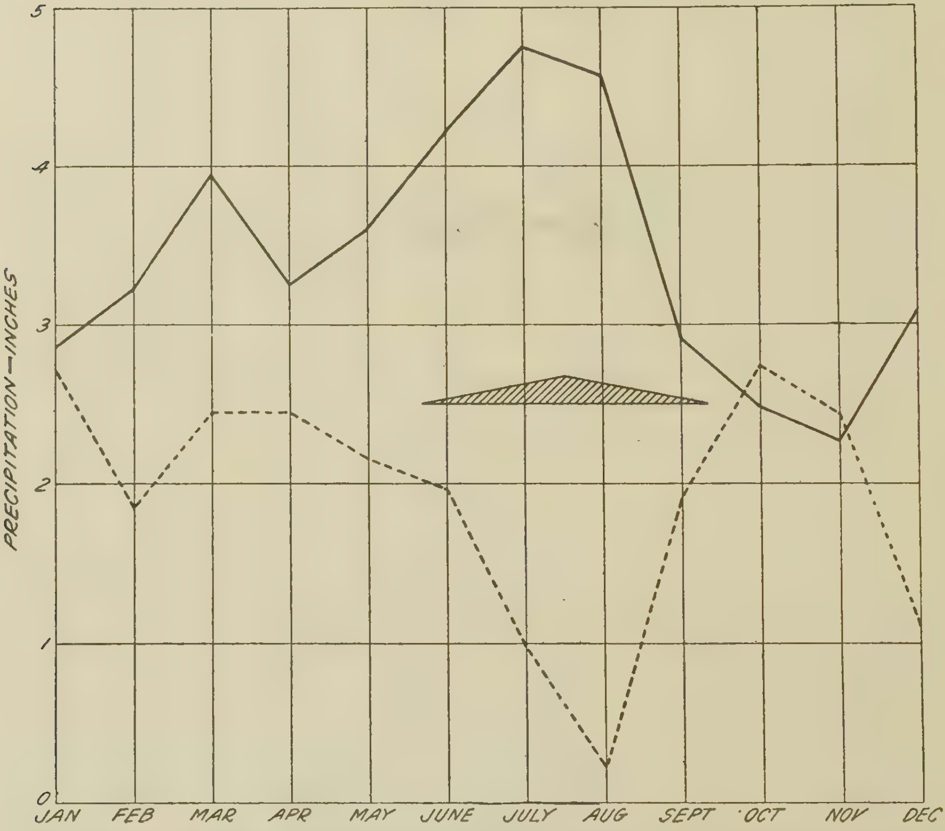

Fig. 43.—Curves of the normal precipitation (black line) and of the actual precipitation for the year 1925 (dotted line) at Asheville, N.C. The shaded area in the centre shows approximately the times of beginning, maximum and the end of the flight of the hickory-bark beetle in 1925. (After St. George, 1929.)

Johnson and Lloyd (1923) in their studies on tsetse flies in Northern Nigeria discovered a connection between the rainfall and the rate of reproduction of the flies, the percentage of gravid females fluctuating between 22% during the wet and 68% during the dry season (see Fig. 44).

Outbreaks of Aphids appear to be greatly influenced by precipitation, though the evidence as to this influence being favourable, or otherwise, is not conclusive. Garman (1927) analysed the climatic conditions previous to, and during, an outbreak of Aphids in Connecticut in 1927, with the result that a correlation was found with the abnormally cool and wet weather of that year. Trägårdh (1917), on the other hand, connected the outbreaks of *Aphis padi*, L., in Sweden in 1911 with the abnormally low precipitation during the summer months. Parker (1915), again, found in the case of the sugar-beet root-louse, *Pemphigus betae*, Doane, that soil moisture is a very important controlling factor (see also Becker and Blunck, 1927; Jarvis, 1927).

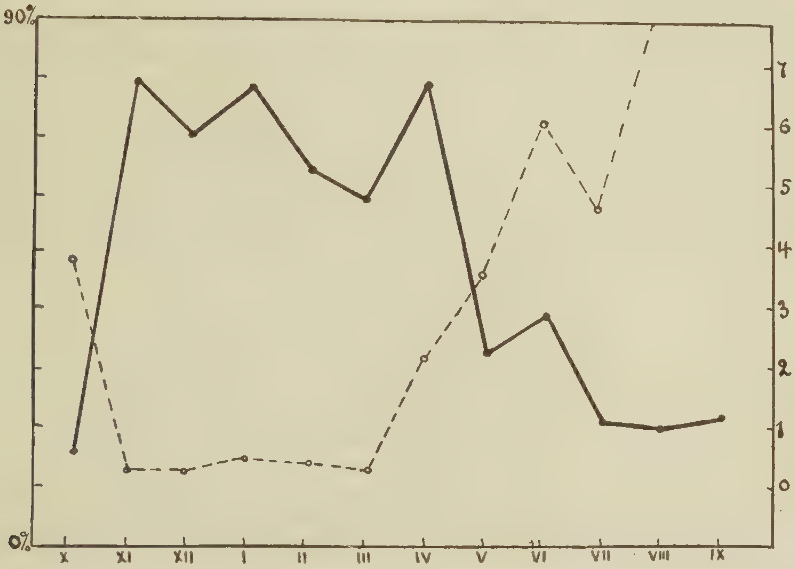

FIG. 44.—The percentage of pregnant tsetse flies (black line; the scale on the left) in relation to monthly rainfall (dotted line; the scale in inches on the right). (Re-drawn after Johnson and Lloyd, 1923.)

(ii) *Deficient precipitation.*

It is clear that drought must be a factor controlling the abundance of mosquitos, the larvae of which breed in pools of water (MacGregor, 1921; Martini, 1923). There are, however, other insects that are dependent on the presence of sufficient moisture for their development. Thus, for the Hessian fly, drought conditions are extremely unfavourable, since the larvae and pseudo-pupae are easily killed by dryness. The adults also die prematurely without realising their productive abilities. Eggs do not hatch successfully, or young larvae are unable to reach the most tender parts of the stem (Znamenskiĭ, 1924; Criddle, 1917). The controlling influence of drought is often indirect, acting through the food-plants. This is sometimes the case with the beet leafhopper, *Eutettix tenella*, Baker, which becomes abundant when there are heavy rains and a sufficient supply of succulent food for nymphs breeding on grasses (Severin, 1924). The larvae of the beet weevil, *Bothynoderes punctiventris*, Germ., during a drought are forced to burrow more deeply into the soil, where they find no food (Pospelov, 1913). The eggs of the Desert Locust, *Schistocerca* *gregaria*, Forsk., can develop only if they are laid in very damp soil, so that their successful hatching depends entirely on a sufficient rainfall at the right moment (Bodenheimer, 1929, 1930).

Deficient rainfall has been reported as favourable for the outbreak of a number of other insects, *e.g.* the nun-moth (Ružička, 1923), the European corn-borer (Barber, 1926), *Bupalus piniarius*, L. (Eckstein, 1923), wireworms (De Gryse, 1929), tobacco thrips (Hooker, 1907; Wardle, 1927), warble-flies (Walton, 1928), chinch-bug (Thomas, 1880; Webster, 1898), and *Pegomyia hyoscyami* (Kaufmann, 1928).

(iii) *Winter precipitation.*

The rôle played by snow-cover in the survival of hibernating insects has been already discussed (see p. 140). Winter rains in climates with relatively mild winters are also of importance in this connection, since we know that the degree of cold resistance in insects is closely dependent on the moisture conditions of their environment. For example, excessive winter rainfall was considered the most important factor in the winter mortality of hibernating cotton-boll weevils by Sanderson (1907), while Ohlendorf (1926) observed a 100% mortality amongst pink bollworms hibernating in an irrigated field.

(iv) *Effects of rainfall in tropical climates.*

Although very little is known of this subject, it appears that the distribution of rainfall throughout the year is a more important factor in the tropics than the total amount of precipitation, probably because the latter is always high. The balance of the coffee-berry borer, *Stephanoderes hampei*, Ferr., in Java depends entirely on the seasonal distribution of rainfall. In certain areas there is rain at all seasons and the flowering of the coffee-plant and the ripening of berries is spread over the whole year, so that the insects always find food, and their generations follow each other continuously. In other districts, the east monsoon brings with it a dry period of several months' duration, and the west monsoon is accompanied by continuous rains, which prevent the flowering of coffee. Thus, a period when no food is available for the pest is interpolated each year, and during this period the beetles die out, with the exception of a few chance survivors (Friedrichs, 1925).

Studies on the sugar-cane froghopper in Trinidad, carried out by Williams (1919, 1921) and Withycombe (1926) showed that even relatively small departures from the normal distribution of rainfall may be of importance. If some rain falls during the dry season, the froghoppers begin to breed, instead of aestivating. A dry spell during the wet season, when froghoppers breed continually, while not increasing the numbers of insects, intensifies the damage to the plants owing to the limited water supply (the actual factors of damage are more complicated; see p. 163).

Outbreaks of *Nephotettix bipunctatus*, F., in Malaya follow abnormally heavy rains, while, on the other hand, in the case of the coconut Zygaenid, *Artona catoxantha*, Hmpsn., rainy weather at the breaking of a monsoon, terminates the outbreak (Corbett and Dover, 1928).

Wolcott (1915) has recorded that in Porto Rico a distinct inverse relation can be observed between the annual rainfall and the damage by the sugar-cane borer, *Diatraea saccharalis*, F. In Southern Nigeria the August rainfall appears to be the chief factor favouring the increase in numbers of several pests of cotton (Mason and Jones, 1924).

(v) *Rainstorms.*

Although rainstorms are not a very common phenomenon anywhere and their controlling influence on insects can only be local in character, there are a few interesting cases on record of high mortality caused by heavy rain.

Barber (1926), in his studies on the European corn-borer, found that a heavy rain may cause a considerable mortality amongst the moths. The influence of rain on oviposition was very important in cages with artificially produced rain, the average number of eggs laid being 1·68 per female, while without rain the number of eggs laid per day was 14. Newly hatched larvae, also, suffered a great mortality from rains, as is shown in Table XXXVII.

TABLE XXXVII.

MORTALITY OF YOUNG LARVAE OF EUROPEAN CORN-BORER, CAUSED BY HEAVY RAIN. (After Barber.)

Number of eggs.	Number of larvae reaching maturity.	
	Heavy Rain.	No Rain.
300	16	74
400	14	63
500	15	106

W. L. Thompson (1928) observed in Florida the effects of a rainstorm on *Aphis spiraecola*, Patch, about 80% of which were destroyed.

Walton (1928) recorded that heavy rainstorms have a considerable value in the control of *Plutella maculipennis*, Curt., the effects being due to the coating of the under surfaces of leaves, where the larvae live, with a layer of mud splashed up from the soil.

(vi) *Hailstorms.*

During his quantitative studies of the insect population of a meadow, Dogel (1924) had an opportunity of observing the controlling effect of a hailstorm. Sample plots, on which 150 Aphids were previously counted, contained on the average only 24 to 36 after a hailstorm. Thrips were affected in a less degree, probably owing to their more retiring habits, the figures being 39 and 33 respectively.

(*d*) **Wind.**

Wind can be an important indirect controlling factor by contributing to the evaporative power of the air. This is the case with the tsetse fly *Glossina palpalis*, R.-D., which is extremely sensitive to low air humidity, and the dry east wind known in French West Africa as "harmattan" causes the fly to concentrate in the densest bush, near water (Roubaud, 1920).

The mechanical action of wind can directly destroy insects, by carrying them to places unsuitable for life or reproduction, and by interfering with their normal activities.

In the natural control of the European corn-borer wind seems to play a fairly important part by preventing moths from ovipositing (Barber, 1926), and by destroying young larvae. The latter are affected even by relatively light, but fitful winds, which cause the larvae to spin down from the leaves to the ground, whence they can seldom reach the food-plant again (Huber, Neiswander and Salter, 1926). The "mistral," a cold north-east wind blowing in the Rhône valley, is a definite controlling factor, since it destroys the young larvae (Thompson and Parker, 1928).

Direct injury to the eggs of the Colorado potato beetle may result from abrasion against the soil during periods of windy weather (Gibson, Gorham, Hudson and Flock, 1925).

It is interesting to note that wind may be injurious even to some insects breeding in water, *e.g.* to mosquitos, the larvae of which cannot breathe regularly if there are strong waves on the surface of the water. Fossey (1911) made an experiment with a ventilator producing a strong motion of air over the surface of a basin containing mosquito larvae. After six hours all the larvae were lying dead on the bottom. This shows why large wind-swept expanses of water are unsuitable for the breeding of mosquitos.

We have discussed in Section VII the rôle of wind in the passive distribution of insects, which can thus be carried for great distances. As a result they are often transported to areas wholly unsuitable for them, as is shown by the example of spruce Aphids carried to Spitzbergen (see p. 117). Drifts of debris usually found on the shores of seas and large lakes are well known to collectors of insects as a good hunting ground, and after a storm such drifts may contain enormous numbers of insects, testifying to the controlling influence of storms. Needham (1900) described such a drift formed on the shores of Lake Michigan after a gale, and stretching for over 50 miles. Insects of nearly all orders were represented in the drift, one square metre of which was found to contain 2520 crickets, 771 grasshoppers, 220 beetles, 75 dragonflies, etc.

An interesting case of the indirect influence of wind on insects is offered by windfalls in forests in relation to bark-beetle outbreaks. It is well known that bark-beetles develop best in trees that have a reduced water content, *e.g.* in freshly cut logs, slash, etc., in which, however, the conditions soon become unfavourable. In the case of windfalls the majority of the trees are merely pushed over, leaving a part of the root system still in the ground, so that the moisture content inside the tree, although reduced, remains favourable for a longer period. Miller (1929) described two areas in California, in which heavy windfalls occurred. In both there were outbreaks of bark-beetle within 2 to 4

TABLE XXXVIII.

MORTALITY OF *CHRYSOMYIA MACELLARIA*, F., UNDER A FALLING AND RISING BAROMETER. (After Parman.)

Date. Nov. 1919.	Temperature F°.		Barometer.		Humidity.		Percentage of mortality.
	Max.	Min.	8 a.m.	8 p.m.	Max.	Min.	
23	75	61	29·45	29·15	93	65	76·2
24	70	55	29·05	28·90	98	87	
26	79	42	29·05	29·00	87	36	11·6
27	54	48	29·25	29·35	98	86	

seasons. In one case, the number of standing trees per timbered section, killed during a normal season, was 25, while in the year following the windfall it increased to 228 (see also Hopkins, 1909).

(*e*) **Atmospheric Pressure.**

Parman (1920) has published a table (see Table XXXVIII) showing that in some flies the mortality increases considerably with a falling barometer, but these data require corroboration in view of the negative results of experimental work on the influence of changes in pressure on the life of insects (see p. 78).

(*f*) **Thunderstorms.**

According to Hopkins (1905, 1909), trees struck by lightning furnish exceptionally favourable conditions for bark-beetles, which breed in them and then infest the neighbouring sound trees.

(*g*) **Temperature and Rainfall.**

It would not be difficult to find in the literature of economic entomology, statements to the effect that cool and rainy weather favours the outbreak of one pest, but controls that of another (see, *e.g.* Berwig, 1926; Faes, 1928, Gasow, 1925; Knoche, 1929; N. Lehmann and Vaney, 1911; Packard, 1929, Sachtleben, 1929, etc.). However, practically all these statements are based on general impressions, and no attempt is made to elucidate whether the controlling influence is exerted by any one meteorological factor or by a number in combination.

Cook's (1923, 1926) studies on cutworms offer one of the best examples of the combined controlling influence of temperature and precipitation. Each of the three species studied proved to have definite moisture requirements, both optimum and limiting. In the case of *Lycophotia margaritosa*, Haw., for example, the optimum condition was found to be about 60% of the total water capacity of the soil. The mortality during the development from the egg to the adult stage was in this case about 80%, while at other humidities it was as high as 93·2%. A consideration of the relationship between temperature, precipitation and soil moisture makes it evident that, since the evaporating power of the air varies with the temperature, a heavy precipitation at a high temperature would result in the same degree of soil moisture, as a lighter rainfall at a lower temperature. For example, the soil moisture at 20° and 70 cm. precipitation would probably be equivalent to that at 15° and 50 cm. of rain. The optimum soil moisture can be expressed mathematically in the form of an equation similar to that representing the relation of the vapour pressure of water to temperature, giving directly the optimum conditions in terms of temperature and precipitation during the growth period of the species. The equation for *Lycophotia margaritosa* was found to be

$$\text{Log}\, y = 0{\cdot}03695 + 0{\cdot}00845\, x$$

where y represents the precipitation and x the temperature.

A study of the mean meteorological data for the area of the distribution of the species demonstrated that the average conditions approach the optimum very closely. This means that outbreaks are liable to occur in years when there is no deviation from the average. Actually, however, some other controlling factors must be considered, particularly the conditions during hibernation. In the case of another cutworm, *Cirphis unipuncta*, Haw., it was found that a warm winter, with light snowfall, is most favourable for the species.

Studies of the climatic relations of the pale Western cutworm (Cook, 1926) also proved that there exists a definite critical soil moisture, depending on both temperature and rainfall. If the moisture exceeds the critical amount, the number of cutworms decreases in the following year; but if the moisture is less than the critical amount, the number of cutworms increases. The effect is cumulative, and severe outbreaks follow a series of dry years.

It is important to note that, as admitted by Cook himself, the physiological reasons for the connection between soil moisture and the abundance of cutworms is still not clear, although his investigations are much more thorough than most entomological studies. Indeed, there is here an almost entirely unexplored field, and work in this direction is likely to be of exceptional value in the study of the relative abundance of insects, especially of those which pass one or other part of their development in the soil.

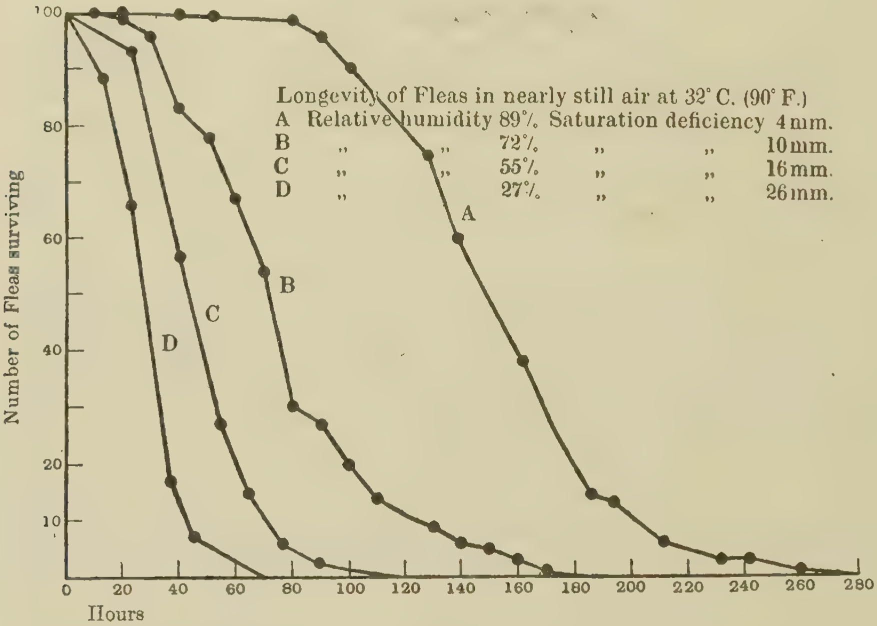

FIG. 45.—The influence of saturation deficiency on the longevity of fleas. (After Bacot and Martin.)

(*h*) Temperature and Humidity.

We have seen in Section IV (p. 81) that there exist definite combined optimum and critical conditions of temperature and humidity for each species of insect. It is natural to expect that the combined action of these factors should have a close relation to the fluctuations in the abundance of insects. Sufficiently exact data, bearing on this subject, are, however, far from numerous.

Epidemiological studies on plague transmitted by rat fleas (Bacot and Martin, 1924; Brooks, 1917; Buxton, 1923; Hirst, 1926–1927, etc.) have revealed a definite connection between plague epidemics on the one hand, and the temperature and saturation deficiency of the air on the other. Experimental work by some of the authors quoted, proved that this is connected with the length of the life of fleas away from their hosts (rats) under varying conditions. The survival of *Xenopsylla cheopis*, Roths., is approximately in an inverse proportion to the saturation deficiency of the air provided the temperature and air movement are constant. In other words, it is proportional to the rate of evaporation (Fig. 45). If the saturation deficiency is constant, the length of life is reduced by from 50 to 66% by a 10° rise in the temperature. A variation of the saturation deficiency from 5 mm. to 35 mm., such as occurs in the plains of Northern India, would, accordingly, shorten the average duration of life of wandering rat fleas in the proportion of fifteen to one (Bacot and Martin, 1924). This accounts for the fact that plague does not maintain itself in an epidemic form when the temperature rises above 26·6°, and is accompanied by a saturation deficiency of over 8 mm. (Brooks, 1917).

Cragg (1922) explains the seasonal prevalence of relapsing fever in India by the reactions of *Pediculus*, which transmits the disease, to a varying climate. The temperature and the humidity in March and April are at the optimum for the insect, and it becomes very active. As the season advances, the optimum is passed, and the extreme heat of May produces a heavy mortality. Epidemics are due to abnormal seasonal variations in temperature and humidity.

The connection between mass outbreaks of Aphids and climatic conditions, as represented by temperature and humidity, has been often mentioned in the economic literature, but apparently so far no exact investigations have been made on this problem.

Some undetermined, but probably climatic causes are responsible for the ratio of sexes in different years, as has been pointed out by Reh (1902) with regard to scale insects. In 1897–98 several species were represented only by females, while in 1899–1900 males were numerous, and in some species even prevalent.

(*i*) **Temperature and Light.**

The activities of certain nocturnal Lepidoptera are regulated by the degree of darkness in combination with the temperature, which should not be below the zero of activity. Copulation and oviposition, both of which usually involve flight, are, therefore, dependent on a favourable combination of these meteorological factors, which, thus, may become of primary value in the control of abundance.

In the codling moth (Isely and Ackerman, 1923) at least partial darkness and a temperature above 16·6° are necessary for oviposition, so that the latter is almost entirely confined to nights in which the temperature is above that limit. If a low night temperature prevails during the flight period of the moths, the number of eggs deposited may be very low and the resulting brood of larvae very small.

Similar relations exist in the case of the nun-moth, *Porthetria monacha*, L., as has been shown by Sedlaczek (1915). Copulation flights are possible only during still, rainless evenings, with a temperature above 15°. A sufficient number of such evenings can occur in Central Europe only after July. If there are more than 12 such evenings, the year is favourable for the increase in the numbers of the moth.

(*j*) **Indirect Effects of Climate.**

(i) *Food.*

Since plants depend on climatic factors for their life and metabolism in no less a degree than animals, phytophagous insects may often be affected by climate not only directly, but also through their food-plants.

An abnormally severe winter that kills off an insufficiently hardy plant will naturally cause the insects feeding exclusively on it to die out. The same may happen in the case of a drought, as in the case of masses of locust hoppers, *Dociostaurus maroccanus*, Thung., dying out in Turkestan from the lack of any green food owing to an abnormally dry spring (Plotnikov, 1917).

When only certain parts of plants suffer from frost, or drought, or other meterological factors, insects with specialised food habits are often affected. If, for example, the flowers on fruit trees are killed by a frost, there will be no food for the insects developing in the fruit; or if cotton sheds its squares and bolls as a result of a drought, the insects dependent on them are subject to starvation.

These are, of course, extreme cases, but there are others that occur more commonly and are therefore of more importance from the point of view of insect abundance. There is, for example, a certain correlation in the time of the seasonal development of an insect and of its food-plant. The rate of development in both cases depends on the weather, but the latter may affect the insect and the plant in an unequal degree. As a result, the normal adjustment of the seasonal cycle of the insect to that of the plant would be destroyed, with serious consequences for the insect.

An example of the indirect controlling influence of weather of this type is offered by the apple-blossom weevil, *Anthonomus pomorum*, L., which lays its eggs in the flower buds. The larva on hatching fastens the petals from the inside and accomplishes its development in this closed chamber. The rate of the development of the flower buds and of the ovaries of the insect depend on the temperature conditions, and normally the beetles are mature and begin oviposition before the buds begin to open. The response of buds to abnormal temperature conditions is, however, not always the same as that of beetles, and it sometimes happens that the buds, of at least some early flowering varieties, are almost ready to open when the beetles start laying eggs. As a result the flowers open before the larvae have had time to fasten the petals, and the larvae fall out (Ritus-Potapov, 1928).

The practice of altering the date of planting, so as to escape injury by pests (Hessian fly, for example), has a definite bearing on this subject, since it is based on the disturbance of the normal correlation between the development of the insect and of the food-plant. The aim of such measures is purely practical, and the fate of the insects deprived in this way of their food has never been studied.

When similar disturbances in the development of plants occur under natural conditions, they constitute an important controlling factor. The disturbance of the correlation between the plant and the insect may often be far from self-evident, since the correlation may be of a chemical character. Thus, the water content of a plant is a factor of great importance for the insects feeding on it, as is exemplified by the cases of bark-beetles (see pp. 132, 141), and Aphids (Garman, 1928). The water content depends, of course, to a great extent on the amount of precipitation and evaporation. Parker (1929, 1930) studied the effects of dry and of succulent foods on the grasshopper *Melanoplus mexicanus*, Sauss., and found that dry food produced a form similar in appearance to the supposed swarming phase (*spretus*, Walsh) of the species. A tabulation of rainfall data for a long period showed that outbreaks of grasshoppers followed a series of dry years (Fig. 46). During the last outbreak in 1922, the grasshoppers tended to vary in the direction of the form *spretus*, probably under the influence of dry food.

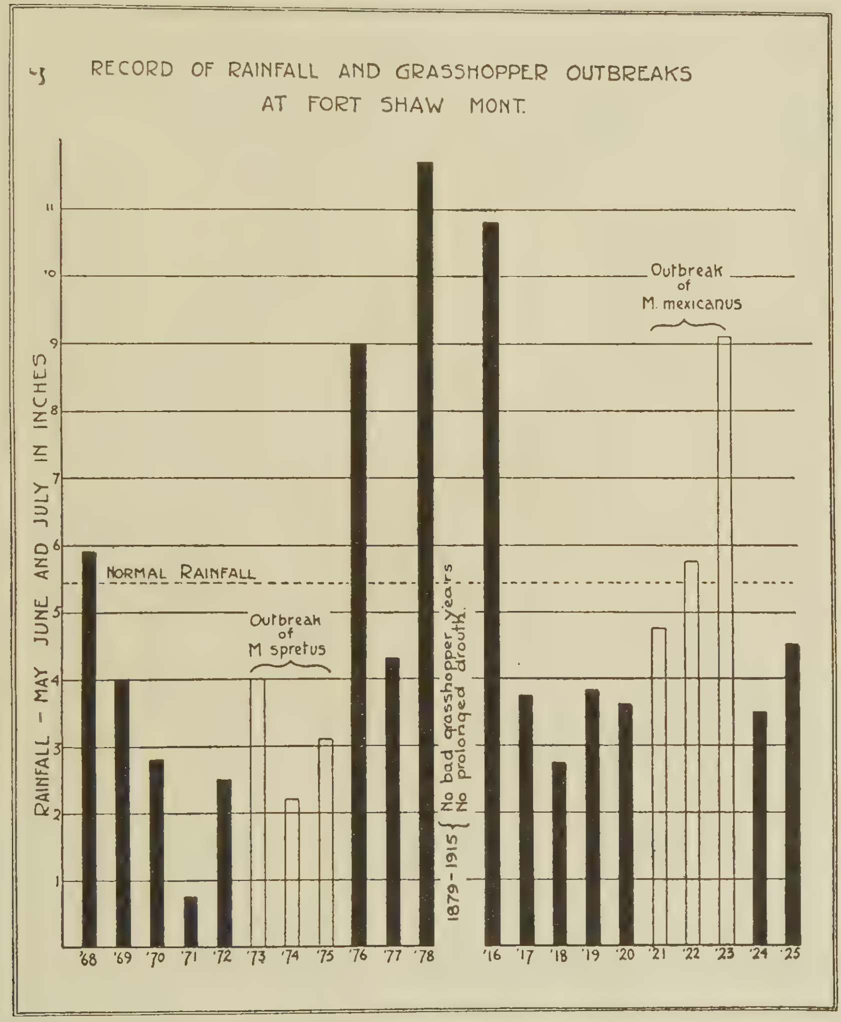

Fig. 46.—Rainfall and grasshopper outbreaks in Montana. (After Parker, 1930.)

It is known, further, that the chemical composition of the leaves of the mulberry tree varies considerably with their development (Maillot and Lambert, 1905). The same must be true with regard to almost any plant, with the result that an insect feeding on it would obtain a food differing chemically from the normal, if the normal synchronism in the development of the plant and of the insect were disturbed by aberrant weather conditions.

These are all mainly theoretical considerations. They are included with a view to attracting attention to the wholly unexplored problem of the climatic control of insects through their food-plants.

(ii) *Natural enemies.*

The common, though never proved, assumption that every organism is perfectly adjusted to its environment, requires a complete agreement between the environmental relations of the insect and its natural enemies, particularly parasites. This means that a host and its parasite should be expected to have approximately the same zero of development and activities, and that they should react to any alterations in external factors by an equal increase, or decrease, in the rate of metabolism. Although this problem has not yet received the attention it deserves, there has already accumulated a sufficient amount of data to show that this is not the case.

Indeed, the fatal limits of an insect and its parasite may be different. Welter (1895) has recorded that the eggs of the silkworm moth can withstand a temperature of −40°, which kills parasites (not specified) inside them. Parasitised beetles, *Psylliodes chrysocephala*, L., withstand low temperatures better than non-parasitised ones, which are more easily killed by frost, with the result that the percentage of parasitised beetles greatly increases towards the end of hibernation (Kaufmann, 1925). Fluctuations in the temperature, also, fatally affect Ichneumonid parasites inside the pupae of *Acronycta aceris*, L., though the pupae themselves survive them. This was observed long ago by Kalender (1872) on bringing the pupae into a warm room in winter.

A well-investigated case of the differential effect of climatic conditions on an insect and its parasite is afforded by the grain Aphid, *Toxoptera graminum*, and by its parasite *Lysiphlebus tritici*, Ashm. (Glenn, 1909; Headlee, 1914; Webster and Phillips, 1912; Shelford, 1926*b*, 1929). The temperature relations of both insects are indicated by curves in Fig. 47 which represent a somewhat simplified version of the curves drawn by Shelford on the basis of Headlee's data. The threshold of development for the host is 0°, while that of the parasite is 2·2°. The rate of development of the host under medium temperatures is on the whole slower than that of the parasite, but above 24°, the rate for the parasite falls off, while that for the host continues to increase. Since the calculated developmental total of the host is 2400°, and that of the parasite is 2933°, at a mean temperature of 20° the parasite would develop in 264 hours, and the host would require 240 hours for its development. While the parasite was developing the host would have produced 26·4 individuals. The parasite would ordinarily sting 22 Aphids during the two days following its emergence, when the total produced by one female of the host would be 31·2 individuals, *i.e.* nine individuals ahead of the parasite (Shelford, *l.c.*). The balance becomes still more favourable for the host at temperatures above 24°, or just above 0°, when all the activities of this parasite are interrupted. It is easy to see that even relatively small discrepancies between the thresholds and the rates of development can become decisive factors in the control of the abundance of an insect.

A similar case is presented by the beet fly, *Pegomyia hyoscyami*, Panz. According to the exhaustive investigations of German authors (Blunck, Bremer and Kaufmann, 1928; Bremer, 1928), the fluctuations in numbers of this pest from year to year are due mainly to the indirect influence of weather. It has been found that low summer temperatures affect the fly less than its parasites, with the result that the number of flies increases during cool summers. Normally warm and dry summers favour the parasites more than the host, and the numbers of the latter are reduced.

Observations on other insects, viz. the nun-moth and Tachinids (Ružička, 1925), Cecidomyids and their parasites (Barnes, 1930), the spider *Epeira gibberosa* and the parasite of its eggs, *Arachnophaga picea*, Riley (Weese, 1923*a*, 1924), etc., corroborate the idea that a host and a parasite are very often unequally adjusted to the normal climatic conditions and react to disturbances in them in a different way, with unexpected results so far as the numbers of the host are concerned.

Seamans (1923) and De Gryse (1929) described a special case of the parasitic control of a pest being regulated by weather conditions. The cutworm *Porosagrotis orthogonia*, Morr., in dry weather feeds on the underground parts of plants, while in wet weather it appears on the surface and feeds on leaves. It is then more exposed to attacks by parasites. The increase in the percentage of parasitised cutworms is definitely correlated with the number of days in May and June having a precipitation of more than 0·25 inch. If their number is under ten, there follows an increase in the numbers of the cutworms. Years with more than 15 wet days result in an almost total disappearance of the pest.

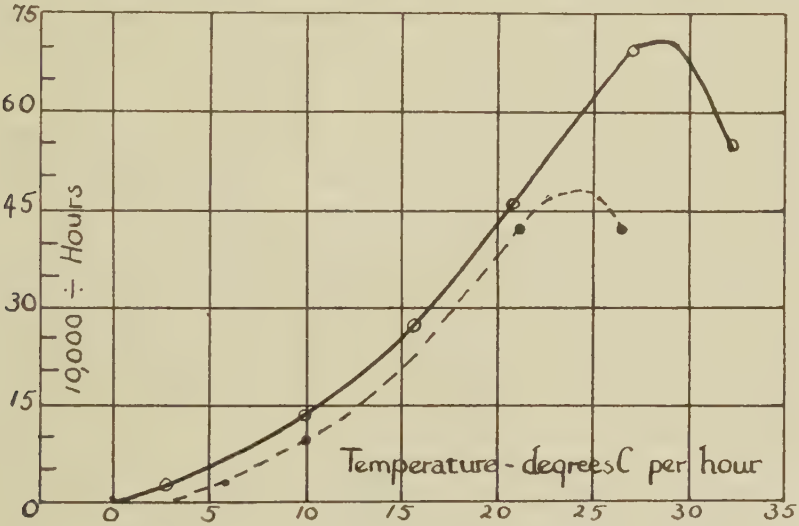

FIG. 47.—The velocity of development curves of the grain aphis and its parasite *Lysiphlebus*. (Redrawn after Shelford, 1929.)

The case of predators regulating the numbers of insects should also be considered. Barrett (1882) suggested that the greater percentage of survival of hibernating insects in cold winters, as compared with mild ones, may be due to the greater numbers and greater activity of predators (birds, moles, etc.) during mild weather. Bertoni (1919) recorded that the abnormally cold winters of 1916–1918 in Brazil resulted in the death of many insectivorous birds from cold or starvation and that an exceptional increase in the numbers of some insects resulted.

Jöhnsen (1930) has presented an interesting study on the relations of

Aphids and the Coccinellids preying on them to temperature conditions. With a rise in the temperature, the amount of food consumed by a ladybird larva increases. At the same time, however, the development is accelerated, and the last larval stage, during which most Aphids are consumed, becomes shortened. Therefore, the total amount of food taken by a larva at a high temperature, is actually less than that taken normally. Such high temperature also increases the rate of the development of the Aphids. In their case, moreover, this results in an increase in the number of generations, and in the number of individuals, which is not the case with ladybirds. Thus, high temperatures, while definitely more favourable for both insects, are much more favourable for one and deprive the other of its controlling power.

An outstanding case of the indirect controlling influence of weather is offered by climatic factors acting on organisms pathogenic to insects. Fungous epidemics amongst locusts and grasshoppers are well known, and they depend entirely on the combination of temperature and humidity favourable for the development of the locust fungus, *Empusa grylli*, Fres. (Uvarov, 1928; a review of the problem). Fungous diseases of other insects show the same close connection with weather conditions. Morrill and Back (1912) who studied the natural controlling factors of ALEURODIDAE in Florida reached the conclusion that their fungous parasites cannot be induced to cause an epidemic if the weather conditions are unfavourable, but that with suitable moisture and temperature an epidemic arises and spreads very quickly. Winter mortality of insects is, also, often due to certain fungi, which develop particularly well during mild winters (Feytaud, 1914). It is interesting, further, to record the observations by Gee and Massey (1912), who found that the normally saprophytic fungus *Aspergillus flavescens*, Eidm., may cause a considerable mortality of apple-tent caterpillars, *Malocosoma americana*, F., if they are kept at 35–37°. This temperature is not beyond the limit of those occurring under natural conditions.

While most parasitic fungi require a fairly high degree of humidity for their development, there are some with different requirements. Pospelov (1913) has recorded, for example, that an extensive drought favours the development of the red muscardine, *Sorosporella uvella*, Krass., on the larvae of the beetroot weevil, *Bothynoderes punctiventris*, Germ.

The influence of meteorological factors on insect diseases due to organisms other than fungi is also very great, though still very imperfectly studied. To quote only a few examples, King and Atkinson (1928) have reported a severe bacterial epidemic of caterpillars of *Euxoa ochrogaster*, Gn., in Saskatchewan in 1925, when, owing to excessively wet and warm weather, the percentage of infected caterpillars rose within a month from 10 to 65. Experimental work by Paillot (1921) and Pospelov (1926) has shown that certain bacilli may be harmless to an organism at one external temperature and cause its death at another. Paillot's experiments were concerned with *Bacillus melolonthae nonliquefaciens*, which on being introduced into the body cavity of larvae of *Euxoa segetum*, Schiff., were bacteriolised at 24°. If the larvae were kept at 10° the bacilli survived. Pospelov worked with *Coccobacillus acridiorum*, d'Herelle, which is a normal, and apparently harmless, symbiont of locusts, but which tends to become a dangerous parasite at a low temperature and high humidity.

The so-called polyhedral diseases of insects, while constituting an important controlling factor, are themselves controlled by weather conditions. Escherich and Miyajima (1911, 1912) found, for example, that a chronic form of polyhedral disease of nun-moth caterpillars can be turned into an acute one by exposure to bright sunshine or cold. This accounts for the fact that epidemics in nature usually coincide with sudden changes in the weather.

Since practically every species of insects is connected not with one species of parasite or predator, but with a number of them, the ultimate effect of a set of weather conditions on the pest is often very difficult to foresee. W. L. Thompson (1928) recorded, for instance, the effects of a hurricane and a rainstorm on a colony of Aphids, which also included larvae of ladybirds, Syrphid flies, etc. All the predators, except the adult ladybirds, were entirely destroyed and the Aphids were reduced by 80%, but on the other hand the storm cleared the colony from fungi, since all Aphids killed by the fungus *Empusa fresenii*, Now., disappeared after the storm. As a result, within a fortnight of the catastrophe the number of Aphids increased to half of that before the storm. Ružička (1925) records that a dry and hot spring reduces the numbers of Tachinids parasitic on the nun-moth, while these conditions are unfavourable to polyhedral diseases.

(*k*) **General Effects of Climate on Abundance.**

(i) *Total value of climatic control.*

We have given a long series of examples of the control of insect numbers by climatic factors. Practically all these cases deal with the destruction of a high percentage of insects at a given stage, or period, while the meteorological factors act on insects throughout their life-cycle, and the aggregate effect must be both very great and very difficult to estimate. Direct and sufficiently exact data on this subject are as yet very scanty, but nevertheless most suggestive. C. Packard (1929), in summarising the work done on the Hessian fly in the United States, enumerated the following meteorological factors controlling this pest. Severe storms and low temperatures control the insect in the susceptible egg, early larval, pupal, and adult stages. Extreme heat and low humidity are very dangerous to all stages except the quiescent puparium. Protracted drought or low temperature inhibit the activities of the larva and of the adult. This series of unfavourable meteorological conditions is so long and so varied that one or more are likely to occur every year, and the chances of the insect surviving are extremely small.

Bodenheimer's (1928) investigations of the almond sawfly, *Cimbex quadrimaculatus humeralis*, Muell., in Palestine show that the mortality, due entirely to climatic causes, reaches 40-90% in the egg-stage, and 80–90% in the larva, while about 10–20% of the pupae are killed by parasites. In this case there is 96% of mortality due to climatic factors.

Kirkpatrick (1923) studied in a most careful way the environmental factors controlling the abundance in Egypt of the cotton-seed bug, *Oxycarenus hyalinipennis*, Costa. Every stage in the development of the insect proved to be affected by climatic factors in a most fundamental way. The losses amongst adults during quiescence which corresponds to hibernation are especially serious. Between 13 and 22 million bugs per *feddan* (1·038 acres) occur at the end of the breeding season, while only about 100,000 are present in the spring. Thus, the normal percentage of survival is between 4·5 and 7·7%. The causes of the destruction are considered by the author to be mainly climatic.

Exhaustive studies of the factors controlling the European corn-borer in Europe, carried out during a series of years by Thompson and Parker (1928), led those authors to the conclusion that control is produced by a complex group of agricultural, meteorological and parasitic factors. However, no definite correlation has been observed between the quantitative or the qualitative composition of the fauna parasitic on the borer and the degree of infestation. Areas in which parasitic species are numerous or parasitism is high are not necessarily those in which the borer is least injurious. Moreover, a parasitic fauna poor in species or causing a low parasitism is not always or even generally accompanied by high infestation and severe damage. The authors believe that the greatest controlling value is attributable to the factors which they call " intrinsic." Under this term they include those characteristics of the structure and habits peculiar to the species, by reason of which a high mortality occurs in certain phases of existence even in the normal environment. In the case of the corn-borer, young larvae are extremely delicate and die from the slightest injury, so that even under normal conditions the percentage of elimination must be enormous. It is obvious that every departure from the optimum conditions of temperature, humidity, etc., every fluctuation of any of these external factors must increase the percentage of eliminated individuals. Thus, the " intrinsic " factors of Thompson and Parker may be interpreted as a highly inefficient adjustment of the insect to environmental conditions, amongst which the first place undoubtedly belongs to the climate.

Several American authors (Hunter and Pierce, 1922; Pierce, Cushman, Hood and Hunter, 1912; Hinds, 1907; Hinds, Yothers and Hunter, 1909; Kincer, 1928) have studied the natural control of the Mexican cotton-boll weevil and have found that in the majority of cases climatic factors are far more important than any other.

Evidence of this kind is only beginning to accumulate, but it is already sufficiently weighty to show the necessity of revising some well-established ideas as to the relative value of the climatic and other factors controlling insect abundance. However, before we enter upon a discussion of this general problem, we must consider some other data relating to the fluctuations in numbers of insects as they occur in nature.

(ii) *Course of outbreaks.*

According to the commonly accepted theory of fluctuations in numbers of an insect, the process is represented as being almost entirely regulated by the interrelations between the insect and its natural enemies. It is assumed that an insect may begin to increase in numbers owing to some favourable (*e.g.* climatic) conditions. Its natural enemies begin then to increase in their turn, and sooner or later their numbers reach the level at which the host is kept in check, the majority of its progeny being exterminated by the enemies. When this happens, the numbers of the host dwindle rapidly, with the immediate result that the enemies are deprived of a sufficient supply of food and their numbers become reduced. When the host is in minimum numbers, the chances of the survival of its parasite, or predator, are very small, and the percentage of hosts killed by them becomes such that the host again begins to increase in numbers.

This scheme is, of course, almost entirely theoretical, and its weakest point is that both the host and its parasites and predators are considered to increase or decrease in numbers only as a result of their interaction, without any relation to the factors favouring the increase or decrease of each of the species concerned. We have seen above that each of these processes is most deeply affected by meteorological factors, and the omission of the latter from the consideration amounts to a deliberate and inadmissible simplification of the problem. It cannot be denied that natural enemies of various kinds can exercise control over insects, thus causing fluctuations in their numbers, moderated or accentuated by climatic influences, acting both on the insect and on its enemies. On the other hand, we have just reviewed a number of cases which show that fluctuations very often occur from causes mainly, or purely, climatic.

The response of an insect species to climatic influences may in some cases be very rapid. This is the case with Aphids, which, owing to their very short cycle of agamic development, can multiply at an enormous rate as soon as the conditions are favourable. Reverse examples of an abrupt termination of an outbreak by unfavourable weather conditions have been quoted above.

Sudden outbreaks occur not only in the case of insects with a very short cycle, like Aphids, but also in cases of other pests. For example, *Aporia crataegi*, L., may be an uncommon insect for a series of years only to appear suddenly one season in large numbers, and to disappear again the next year (Bremer, 1928). This is a case of an acute outbreak, which it is theoretically impossible to explain by a balance between the host and its parasite. The causes may well be entirely due to the weather acting on the generation involved in the outbreak.

A more common type of fluctuation occurs when a species, not particularly numerous normally, begins to increase in numbers during several successive generations, reaching a maximum and then decreasing again in the course of several generations. This type may be conveniently termed a *gradation*, although this term is applied by German authors to any type of fluctuation. An example of a gradation is offered by the pine moth, *Panolis flammea*, Schiff., which in the first year increases in numbers only slightly, in the second year the increase becomes noticeable, and in the third there occurs an outbreak. Friedrichs (1930) adopts the terms *preparatory* year, *prodromal* year, and year of the " eruption " (it would be better to call this an *outbreak*), for the three successive seasons, fixing in this way the nomenclature already used by several German authors (Escherich, Bremer, Berwig). Sometimes the outbreak year may be followed by one or two years, during which the numbers do not decrease considerably.

Sooner or later, however, the decrease takes place. It is worthy of special note that very little attention has been paid in epidemiological studies on insect pests to the factors causing the termination of gradations, apart from cases in which this is brought about by a catastrophic event, such as a fungous disease. The necessity of studying all the factors of outbreaks and of gradations throughout their full course is too obvious to be insisted upon.

A peculiar feature of the gradations of many insects is that a species, when in large numbers, becomes less restricted ecologically than is usually the case. The case of locusts, *Locusta migratoria rossica*, Uv. & Zal., in Central Russia, investigated in detail by Predtechenskiĭ (1928), is particularly illuminating in this respect. The species normally breeds there only in certain habitats, which are the driest and the warmest in the region. After a series of abnormally dry and warm years the locusts increase in numbers and invade other habitats as well, only to re-assume their " island " distribution on the return of weather conditions normal to the area.

Such *reservations*, particularly suitable for a given species, owing to their ecoclimatic conditions, are a factor of great value in its survival throughout unfavourable years.

The ecoclimates of reservations deserve special attention, since it stands to reason that their conditions are most favourable for the species in a given climatic area. This means that, should the climate throughout the area become similar to the ecoclimate of the reservation, a gradation may be expected to begin.

The value of ecoclimatic conditions is evidenced by observations of Ružička (1927) on the outbreaks of the nun-moth, which, during the generally cool climatic periods, becomes a pest of warm pine forests, while normally it is a pest of spruce forests which are relatively cool.

It is usually assumed that the numbers of an insect species, while increasing during a gradation, return in the intervals to what is called the normal number, which is considered to be more or less constant. There is no evidence, however, that this is actually so. Indeed, it appears that the conception of a normal number is a fiction, since the total population of a given area and habitat is never stabilised and the ratio of its component species fluctuates continually, though the smaller fluctuations cannot be observed except by the use of quantitative methods of study (see p. 172) throughout a series of years. There is, of course, always a certain *average* relative number of each species, but this is only a mathematical average, not actually existent in nature.

(iii) *Periodicity of outbreaks.*

The fact that gradations and acute outbreaks of a number of pests occur in more or less regular cycles of years has attracted the attention of many authors. Swinton (1883) was one of the first to pay particular attention to the problem, with special reference to locust outbreaks. He worked on a purely chronological basis, *i.e.* by compiling the literature data on locust outbreaks in various countries and comparing them with the periods of fluctuation in the sun-spots. His general conclusion was that outbreaks of the Rocky Mountain Locust, *Melanoplus spretus*, Walsh., as well as of other locusts in Africa and in Europe, often, though not always, coincide with the sun-spot minima. Recently, Kulagin (1921) attempted to use the same method for elucidating the periodicity of outbreaks of locusts in Europe, during the eighteenth and the nineteenth centuries, but obtained contradictory results. The failure to secure definite conclusions in the case of locusts may be, however, due to the obviously incorrect method used. Neither author tried to find a definite periodicity in the outbreaks of one particular species in one climatic area. They used data applying to a number of species, each with its own optimum requirements as to the meteorological factors. If we assume, and it appears perfectly reasonable to do so, that the periodicity of outbreaks depends on the periodic fluctuations of the climate, it is obvious that not all the species of locusts in every country can be expected to respond to the fluctuations in exactly the same way and at the same time.

Simroth (1908, 1909) applied the idea of climatic periods caused by the 11-year sun-spot periods to the fluctuations in numbers of various animals, including insects. The evidence collected by him showed that not all the species respond to the fluctuations in sun-spots in the same way, and that the influence of the fluctuations is not felt equally in all countries, but mainly in those where the climate is affected in the greatest degree by the differences in the area of the sun-spots.

Simroth's papers created a considerable amount of discussion. Schröder (1909), Meyer (1909) and Dieroff (1911) published supplementary evidence in support of the 11-year period. For example, the butterfly *Colias croceus*, Fourc., a southern species, appears in more northern localities of Europe only in certain years, separated by approximately 11-year periods. The same applies to the Death's head moth, *Acherontia atropos*, L., which extends its northern limits of distribution about every 11 years.

Meissner (1909) and Schuster (1909) criticised Simroth's theory and published some data in support of their contention that the periodicity of insect outbreaks has no connection with sun-spot periods. Schuster compiled the data on the outbreaks of a number of pests in Germany, with the result that during the 84 years (1824–1908) covered by his records there were only 21 years without outbreaks of one or another insect pest. He concludes from this that there is no periodicity of the outbreaks, but this criticism is valueless, since it is based on the fallacious assumption that all insects should be expected to respond to climatic fluctuations in exactly the same way.

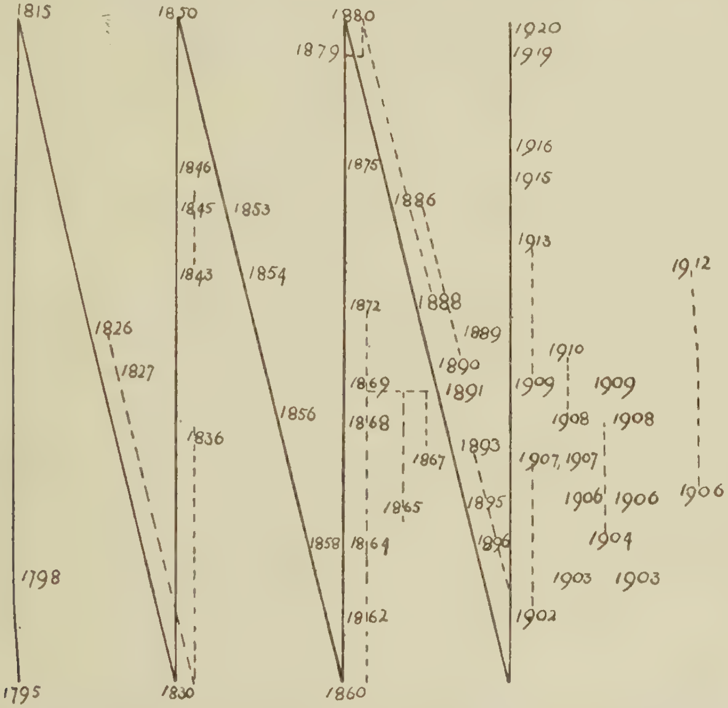

FIG. 48.—Graph showing the relation of outbreaks of *Tortrix viridana* to climatic periods. The black line represents diagrammatically the fluctuation from cold-damp (top) to dry-warm (bottom) climatic periods. The dates are those of outbreaks which occurred mainly in, or about, dry-warm periods. (Redrawn after Gasow, 1925.)

Gasow (1925) has recently studied the records of the outbreaks of *Tortrix viridana*, L., for about 200 years back, and found a fairly close agreement with the 17-year alternating periods of the dry-warm and moist-cool climate established by Supan (see Fig. 48). The outbreaks do not always coincide with the warm periods, but the majority of them fall near the centres of such periods.

All these data are, of course, far from being conclusive as regards the actual length of periods and the regularity of their recurrence. However, the fact that the fluctuations in the numbers of certain insects coincide to some extent with the 11-year sun-spot periods can scarcely be disputed. Seven-year periods were claimed by G. Engelhardt (1926) for swarming of *Celerio lineata* in Ecuador.

Further, there remain such facts as, for example, the synchronisation in the mass appearance of the Desert Locust, *Schistocerca gregaria*, Forsk., in the enormous area stretching from Morocco and Senegal to Kenya, Egypt, Palestine, Persia and Northern India. The locust in question swarmed over the whole of that area in 1915–1916, and a new period started again in 1927 and has continued up to the present time. It will be seen that the interval was a little over 11 years, while the practically simultaneous beginning of the swarming in a number of widely separated countries suggests the existence of a general cause. This cause can only be sought in general climatic fluctuations, connected perhaps with sun-spots but not with local conditions.

(iv) *Ecoclimatic succession.*

The phenomenon of the continuous development of biocoenoses (ecological units, comprising both the vegetable and the animal population of a habitat) leading to their gradual transformation into other types is well known and is termed ecological succession. When a forest encroaches gradually upon grassland, the flora, the fauna and the ecoclimate, undergo parallel changes. Those insects of the grassland which are able to live under forest conditions will be subjected to a new ecoclimate, and this may prove to be either more, or less, favourable to them. It is recognised that the ecological succession goes on everywhere, until a climax biocoenosis (*i.e.* one corresponding best to the existing climate of the country) is formed. Accordingly, the ecoclimatic succession should also go on continually and the average ecoclimatic conditions of any habitat are not constant, but follow a definite trend of changes.

(v) *Geological succession of climates.*

The climate of every area on the surface of the earth has undergone a long series of great changes throughout geological history. We know of the former existence of a subtropical climate in areas which are now the temperate regions of the earth. We know of the glacial period, or periods, which occurred in the same regions. There are suggestions based on very convincing evidence of a dry and hot (xerothermic) period probably following the glacial one. This geological succession of climates has left the deepest impression on insects, both as regards the present geographical distribution of species and of whole groups, and their bionomic peculiarities. Certain groups of subtropical insects died out in northern latitudes when the climate became colder, while others responded to the winter cold by adjusting their annual cycle accordingly, and by adopting the habit of hibernation. We have shown above (see p. 124) that this habit can be acquired as a direct response to changed conditions.

An analysis of all the effects of geological changes in climate on insects is beyond the scope of this work (see H. Kolbe, 1912, 1923; W. Schuster, 1909), but I have taken the opportunity of pointing out that the present climate of each country is not constant, but is only a stage in the continuous evolution of climates.

(*l*) **Balance in Nature.**

The theory that all living organisms are in stable equilibrium so far as their relative numbers are concerned is widely recognised to-day. When this theory is applied to the fluctuations in numbers of an insect species the process is represented as follows. If the environmental (*i.e.* climatic) conditions are at all favourable for the insect, it begins to increase in numbers, with the result that there is more food for its predators, parasites and disease-producing organisms, while the amount of food available for the insect itself decreases and the competition between its individuals becomes more acute. An increase in the numbers of all the natural enemies of the insect follows. They gain ascendancy over the insect and cause a decrease in its numbers, leading to a shortage of food for the natural enemies and the reduction in their numbers. The insect then again begins to multiply. This process is usually compared with the movements of a pendulum, the vertical line representing the average or normal condition.

This theory of a stable equilibrium in nature is, however, in direct contradiction of the facts. While it is true that an increase in numbers of a species is usually only temporary, and that a decrease will, sooner or later, follow, there are no proofs that the fluctuations in the two directions are of an approximately equal magnitude, as in the case of a pendulum. Nor is the so-called normal number a constant. We know that some species become gradually more numerous or expand their area of distribution, while others die out. We know that whole biocoenoses undergo a continuous change, *i.e.* an ecological succession, which represents only a short phase of the much longer process of geological succession. To speak of a stable equilibrium in nature, and to compare the fluctuations in numbers of organisms with the regular movements of a pendulum, always returning to a non-existant " normal " condition, is contrary to common sense and amounts to a denial of organic evolution. We may compare the course of the existence of a species to a pendulum in motion, but we must introduce two corrections. The first is that the fluctuations of such a pendulum are entirely irregular, both as regards their velocity and their magnitude in either direction. The other correction is that the pendulum is not suspended from a fixed point, but that the point itself both fluctuates irregularly, and moves with an unequal velocity along an unknown and apparently irregular course. These corrections which are absolutely necessary make the theory of a stable equilibrium in nature and its comparison to a pendulum appear wholly artificial.

As has been pointed out above, the theory of stable equilibrium is based on the assumption that the numbers of an organism depend mainly on the numbers of their enemies and on the quantity of food, *i.e.* on factors which in their turn are dependent on other organisms. No one will deny the controlling value of these factors, but the evidence collected in this section, as well as in the whole of this paper, should go far towards proving that the key to the problem of balance in nature is to be looked for in the influence of climatic factors on living organisms. These factors cause a regular elimination of an enormous percentage of individuals under so-called normal conditions, which in fact are such that insects survive them, not because they are perfectly adapted to them, but only owing to their often fantastically high reproductive abilities. Any temporary deviations in the climatic factors, however slight they may be, affect the percentage of survival, either directly, or indirectly (through natural enemies and food-plants), and thus influence abundance. Further, the ecoclimatic succession and the geological succession of climates favour the survival and the relative abundance of some species, and condemn others to a complete extermination. Of course, the food, the natural enemies, the competition between individuals and between species, all play their part in these evolutionary processes, but none of these factors are independent and primary in character, since they themselves are deeply affected by climate. It is possible to imagine an insect with no natural enemies and without any need to compete for food, shelter, etc., and there is no doubt that this, if not very commonly, does actually happen in nature, but an insect living under natural conditions and yet free from climatic influences is an absurdity. The fact that the vast majority of entomological investigators do not appreciate this point and continue to study living insects as only partly dependent on climatic factors, or even ignoring these factors altogether, accounts for the very slow progress achieved in the understanding of the life of insects, and of the great problem of natural balance. This balance is intimately connected with the dynamic process of the evolution of species and biocoenoses. It is a balance resembling that of a cork floating on the surface of a running stream, with its whirlpools, eddies and back currents, while the wind blowing with a varying force now ripples the surface gently, now causes it to rise and fall in great waves. The cork rises and falls with them, comes into collision with other floating objects, now rides on a calm surface and is dried by the sun, now is again rolled over and over by a storm and is beaten by rain, but always continues its journey with an ever-changing velocity and along a fantastically tortuous course. We are very far from knowing the causes of evolution, and understand as yet very little of its mechanics. Whether its direction is determined by some inner laws of organic growth, or by the interplay of external forces, will not be discussed here, but there is no doubt that amongst the forces which must influence the direction of the whole process, and particularly of its temporary phases, the first place belongs to climate as an environmental factor from which there is no escape for any living organism.

To study the dynamic balance of a species without taking into full consideration its climatic environment, is an utterly unscientific procedure, though one still commonly applied in entomological investigations. It is true that there are many entomologists who realise the importance of the climatic factor in insect life, but the practical difficulties in studies of this kind are very great, and are more often avoided than overcome.

In the next section it is intended to show the main principles and methods which can be applied to the study of climatic influence on insects, particularly from the point of view of the quantitative analysis of factors, and their effects, with a practical end in view, viz. that of forecasting the course of events in the life of insects as far as it depends on climate and weather.

IX. CLIMATE AND WEATHER IN ECONOMIC ENTOMOLOGY.

(*a*) Climate and Injury to Plants.

The economic importance of an insect in agriculture depends on the amount of damage it causes to plants. While this amount normally increases with the numbers of the injurious insects present on the crop, the relation between damage and numbers is often far from being directly proportional. This disproportion is due mainly to weather conditions.

(i) *Number of generations.*

If the crop in question is liable to attack throughout the season, the damage increases with the increase in the number of generations of multivoltine insect pests in a season. The number of generations in such insects depends on weather conditions, and especially on the temperature. For example, the codling moth is of relatively little importance in countries with a short summer where only one annual generation is produced, while the damage it does in warmer climates, with several annual generations, is very great.

The number of generations does not always increase with the temperature. Thus, the sunflower moth, *Homoeosoma nebulella*, Hb., normally produces in South-Eastern Russia one complete generation each year, but a certain percentage of caterpillars produce pupae and moths without a diapause, so that a partial second generation is produced. The percentage of transforming caterpillars is greater in cool and moist summers, when the damage increases correspondingly (Sacharov, 1925; see also Kuwayama, 1929).

Examples of this kind could be multiplied almost indefinitely, but there is no need to elaborate this simple proposition.

(ii) *Condition of plants.*

Plants are affected by weather conditions just as much as insects, and a plant weakened by unfavourable conditions of growth is liable to suffer more heavily from attack by the same number of pests than a healthy one. This is brought out very clearly in the case of leaf-eating insects. If the moisture and temperature are favourable for the growth of a plant, the mass of the foliage is greater and the same amount of it destroyed by insects would constitute a smaller percentage of the whole, while a plant which is suffering from drought and is under-developed may be deprived of all its foliage by the same number of the pest and succumb.

In the case of sucking insects, the damage is also most intimately connected with the weather. The "blight" of sugar-cane caused by froghoppers in Trinidad is intensified by dry spells during the wet season, as a direct result of the reduced water supply to plants. Excessive rain, on the other hand, causes a temporary water-logging of soil, the physiological result for the plant being equivalent to the water-shortage. Thus, both drought and excess of precipitation intensify the damage (Williams, 1921; Withycombe, 1926).

Again, the recovery of damaged plants depends largely on the weather conditions. For example, the recovery of wheat plants damaged by frit-fly depends on the ability of the plant to replace by secondary shoots the main shoot killed off by the larvae of the fly. The production of these secondary shoots is only possible at the optimum conditions of temperature and humidity, and in dry years the same percentage of infested plants results in a far greater loss than in wet years. For the same reason, the recovery of wheat plants from the damage by frit-fly is normally more complete in the northern provinces of Russia than in the southern steppes (Znamenskiĭ, 1926). Many examples of this kind could be given, but the case is too well known to economic entomologists to require elaboration (see also Leach, 1927).

(iii) *Phenological adjustment.*

We have seen (p. 150) that a disturbance of the normal parallelism in the seasonal development of an insect and of its host plant may be disastrous for the former. Still more important is this parallelism for the extent of the injury inflicted.

In the case of insects, such as wireworms, or mole-crickets, which cause damage to seeds before and while they germinate, any factors likely to retard the development of the seeds increase the percentage of damage. A cool spring, therefore, while not necessarily being more favourable to the pests in question, is unfavourable to the crop (see also on this subject R. Webster, 1924).

An interesting case has been brought forward by Felt (1916) with regard to the injury of apples by the codling moth. Normally, as is well known to economic entomologists, the newly hatched larvae enter the apple through the calyx and this habit facilitates the control by spraying. However, if a larva hatches after the calyx is closed, it enters the apple anywhere causing "side-injury," and the chances of poisoning the larvae in this case are very small. The time of hatching depends on that of oviposition, and the latter is possible only on evenings with a temperature above 16·6°, so that in a cool spring, or in cooler localities, the percentage of "side-injury," and of damage generally, increases. On the other hand, in the case of the larvae of the codling moth developing in walnuts, the damage is heavier when moths appear earlier and the nuts develop later than usual (Flanders, 1926).

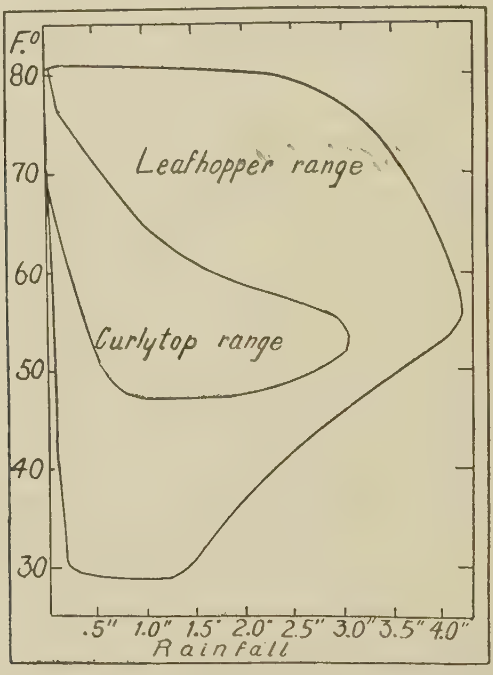

Fig. 49.—Normal thermohyetic limits of the geographical ranges of beet leafhoppers and "curlytop" disease. (After Tehon, 1928.)

Kleine (1920) has pointed out that the caterpillars of the bean moth, *Grapholitha dorsana*, F., can bore into beans so long as they are still sufficiently tender. Any factors, therefore, which tend to accelerate the development of beans, reduce the damage.

Facts of this kind are too numerous to be quoted. Indeed, the well-known method of reducing the damage from insects by breeding "immune" varieties of plants is based largely on the selection of varieties with the seasonal cycle of development unfavourable to the insect in question (see also p. 183).

The cases of the damage caused by insects not directly, but acting as transmitters of diseases of the plant are more complicated. Tehon (1928) studied in a most thorough way the effects of weather on the "curlytop" of sugar-beets, a virus disease transmitted by the beet leafhopper, *Eutettix tenella*, Baker. The range of the leafhopper is much more extensive than that of the disease which it transmits (Fig. 49). A comparison of the climatic conditions over the range of both shows that the difference is mainly due to the amount of the summer rainfall, the absence of precipitation being necessary for the development of the disease. On the other hand, leafhopper abundance is determined mainly by the weather conditions of January and February, when hot or warm weather is necessary for the insects (see also Wille, 1929, on the subject of the virus disease of sugar-beets in Germany transmitted by the bug *Piesma quadrata*, Fieb.).

(*b*) **Climate and Insect-borne Diseases of Man.**

The distribution and the incidence of epidemic diseases transmitted by insects depends on several factors, first the occurrence and the relative abundance of the carrier, and secondly the conditions favourable for development of the micro-organism causing the disease. There may be other, less regular, but none the less important, factors contributing to the development of an epidemic, but it is not proposed to discuss them all.

The literature on the epidemiology of insect-borne diseases is enormous, and the following summary does not pretend to be complete, but is intended to present only some examples relating to the influence of climate on the epidemics (a very good survey of this problem has been made recently by Martini, 1929*a*).

(i) *Malaria.*

The distribution of mosquitos transmitting malaria and their seasonal abundance are determined by the favourable temperature conditions and by the presence of breeding places, which depend to a great extent on precipitation (with regard to the amount of snowfall as a factor in mosquito abundance, see De Gryse, 1929).

The presence of mosquitos does not necessarily render a locality dangerous from the point of view of malaria, since the conditions favourable to the development of the malarial organisms in mosquitos differ considerably from those favourable to their hosts. The lower limit for the development of malarial parasites has been determined as about 15–17°, with the optimum about 22–30° (Gill, 1921, 1921*a*; Grassi, 1900; Grassi, Bignami and Bastianelli, 1899; Jancso, 1904, 1921; W. King, 1917; Martini, 1929, 1929*a*; Mitzmain, 1917; Roubaud, 1918*a*; Sergent, 1919; Wenyon, 1921, 1926, reviews the literature on the factors influencing the development of malarial parasites). This limits the distribution of endemic malaria to countries having a suitable climate, although the mosquitos occur much farther to the north. A reverse case is that of *Anopheles maculipennis*, Mg., and tropical malaria. At temperatures which are under-optimal for the organism of the latter, the mosquito exhibits an abnormal mortality from heat, and the tropical malaria depends for its transmission on other species of mosquitos less affected by tropical climate.

Opinions differ on the question whether humidity conditions directly affect the malarial organism. Bentley (1911) found a direct correlation between the infection of mosquitos and relative humidity, and this has been corroborated by Gill (1921, 1921*a*) and by Mayne (1928, 1930), but Wenyon (1926) thinks this factor of no importance.

Still another factor in the transmission of malaria is the regulation of the activity of mosquitos by the temperature (see pp. 88, 90), by the relative humidity of the air (see p. 94) and by the wind (see p. 97).

The great importance of climatic factors to the organisms causing malaria and those transmitting it finds its practical expression in the epidemiology of malaria. An epidemic of malaria can only develop if all the conditions are favourable both for the insect and the parasite. This optimum condition depends mainly on the combination of temperature and humidity, and this causes the curious phenomenon that in more northern countries malaria epidemics occur mainly in warmer years, while in the south they coincide with cool and wet years. This contradiction is only an apparent one. In northern countries there is always sufficient humidity and mosquitos are abundant, but it is only in exceptionally warm years that the malarial organism can develop there successfully. On the other hand, the temperature conditions in southern countries are always favourable for the parasite, but the breeding of mosquitos in sufficient numbers depends on abundant precipitation. In some situations, however, the case is again different, *e.g.* where malaria is transmitted by species of mosquitos breeding not in stagnant pools, but in running streams. Here the excessive rainfall causes the streams to swell and mosquito larvae are carried away, so that epidemics can develop only in dry years (Martini, 1929*a*).

The climatic relations of malaria are further complicated by the fact that mosquitos feed not only on man, but on domestic animals. Cragg (1923) explained the epidemics of malaria in India after heavy autumnal rains following a drought, by the reduction in the numbers of cattle during the droughts. When the number of cattle is reduced and the number of mosquitos rises owing to the abundance of breeding-places, the conditions are particularly favourable for the transmission of malarial parasites from man to man.

(ii) *Plague.*

The areas of the distribution of epidemics of bubonic plague are confined to countries with hot climates, there being a definite connection between the mean winter temperature and the possibility of epidemics. The reason for this lies in the inability of fleas to survive severe winters (Robertson, 1923). It has, however, been proved by the investigations of a number of authors that the presence and abundance of infected rat fleas is not the only condition necessary for an epidemic of plague. The period of the survival of fleas away from their host is a factor of primary importance, since the longer an infected flea can survive after leaving a dead rat, the greater are the chances of its finding and infecting a new host, whether a rat or a man. Investigations on the longevity of fleas under varying laboratory conditions (Bacot, 1914; Bacot and Martin, 1924; Hirst, 1926–1927) show that the life of fleas separated from their hosts is affected unfavourably by high temperature and low humidity, the same factors also reducing the rate of their multiplication.

Epidemiological studies of bubonic plague in India (Brooks, 1917; Gloster and White, 1917; Goyle, 1928; Kunhardt and Taylor, 1915; Taylor and Chitre, 1923, etc.) have been very aptly summarised by L. Rogers (1928) as follows. The life of fleas is five times as great in August, when the relative humidity at 8 a.m. is 80%, than at 45% humidity in April and May. Studies of the seasonal incidence of plague in different parts of India showed that a temperature of 30° caused a more rapid disappearance of plague bacilli from the stomach of the fleas and reduced their power of infecting animals than did a temperature of 21°. With the low mean temperature of 10° a large number of the infected rats died before plague bacilli appeared in their blood, so that their fleas had no chance of becoming infected. Brooks (1917) correlated the incidence of plague in India with the saturation deficiency, the latter term indicating " the difference between the actual tension of aqueous vapour present in the atmosphere at the temperature in question and the tension of aqueous vapour that would be present in a saturated atmosphere at the same temperature." It is thus a measure of the drying capacity of the air, and Brooks concluded that one degree of dryness indicated by a saturation deficiency of 0·300 inch (mercury) suffices to prevent plague continuing to be epidemic if the mean temperature is also over 26·6°; and that a high saturation deficiency rapidly brings an epidemic to an end even with a temperature over 26·6°. An epidemic may, however, commence and increase with a temperature over that point if the saturation deficiency is below 0·300 inch.

It may be mentioned, further, that a high temperature increases the activities of fleas, including their feeding, so that the intake of infected blood increases accordingly, while the rate of multiplication of the plague bacilli in the rat is also accelerated (Hirst, 1926–1927). As regards the survival of the plague bacilli in the host, the temperature, according to Golov and Ioff (1927), does not exercise any influence, the bacilli surviving as long as the flea is alive.

The investigations on plague have already rendered very valuable practical results regarding the possibility of forecasting epidemics (see p. 176), but there are still many aspects of the problem which require further study. Thus, very little attention has been paid to the actual conditions of the existence of fleas, *i.e.* to the microclimate of their habitats in the larval and the adult stages. Indeed, all attempts to correlate epidemics with climatic conditions are based on the standard meteorological data. It is only recently that Ingram (1927) pointed out that the conditions to which fleas parasitic on wild rodents, living in deep burrows, are subjected, are essentially different from the general climatic conditions of the area. I would suggest that the existence of bubonic plague in the Caspian steppes with their exceedingly severe winters and hot and dry summers may be correlated with the fact that plague is there transmitted not by fleas of the domestic rat, but by those parasitic on wild rodents (susliks, *Spermophilus*, spp.), hibernating in burrows where the fleas are perfectly protected both from winter cold and summer drought.

(iii) *Other diseases.*

The areas of the trypanosome diseases of man and domestic animals in Africa are determined by the climatic and ecoclimatic requirements of the trypanosome carriers, the tsetse flies. Several species of tsetse are involved and each has definite requirements, particularly as regards air humidity (see p. 130). Accordingly, the "fly-belts," as the areas of the occurrence of tsetse flies are called, are essentially dependent on the presence of a certain type of vegetation assuring a favourable ecoclimate (see Roubaud, 1909; Jack, 1917; Swynnerton, 1921, etc.).

The restriction of yellow fever to hot countries depends on the fact that the causative organism does not develop in the mosquito at temperatures below 20°. Similarly, filariasis does not occur in Europe beyond latitude 40° N., although it would find carriers (mosquitos) up to 65° N.; and this is due to the fact that *Filaria bancrofti*, Cobbold, requires a high temperature for its successful development in the mosquito (Martini, 1929*a*).

Cragg (1922) explains the seasonal prevalence of relapsing fever in India by the fact that its carrier (*Pediculus*) finds optimum conditions in March and April, while later in the season the lice are subject to a heavy mortality owing to the heat. Abnormal seasonal variations in the temperature and humidity lead to epidemics.

(*c*) **Bioclimatic Studies on Insect Pests.**

(i) *Physiological life-history.*

We have learned from the previous sections how far-reaching is the influence of the physical factors on all phases of insect life. No study of a living insect can therefore be considered at all complete, unless it comprises a thorough estimation of the value of each factor for each period of the development and for each kind of its activities. Papers on the bionomics of insect pests usually present their life-history in the terms of calendar dates of the appearance of stages, which have practically no meaning and convey no idea of the actual factors influencing the rate of development and activities, as well as limiting the distribution of the insect.

The study of each insect should begin with the elucidation of what Shelford (1920) suggested should be called the physiological life-history, defining the term (1929) as " the life-history of an organism as controlled by its physiological reactions, either spontaneous, or responses to the environment." A physiological life-history can be worked out by direct observations in nature, provided that exact measurements are taken of all environmental factors throughout the development of the insect and until its death. By this method, however, no sufficiently exact information can be obtained as to the influence of each factor, since it is impossible to separate them in nature. The experimental physiological work of testing the value of each factor becomes, therefore, absolutely necessary. This work involves the use of complicated apparatus for controlling the conditions of the temperature, humidity, light, etc., but we need not enter into its description here since this has been done quite recently and in a very thorough manner by Shelford (1929).

The aim of this experimental work is to determine (1) the degrees of the individual factors, and of their combinations, which may have a limiting influence on the insect, *i.e.* which shorten its life, reduce its fertility, etc.; and (2) the rate of the development and of activities under definite environmental conditions. This is possible only by running a series of experiments under controlled conditions at each stage in the development of the insect. Of course, the conditions of the experiments should correspond as closely as possible to those which the insect is likely to encounter in nature. From this point of view, experimental studies on the effects of varying temperatures are particularly important.

The technical difficulties presented by experimental work on physiological life-histories are very great, and it is not surprising that so far such work has only been attempted in the case of a very small number of insects. The pioneer work in this direction has been done by Pierce (1917), who, on the basis of extensive experimental work on the cotton-boll weevil, constructed a chart (see Fig. 22, p. 82) showing the influence of every combination of heat and humidity on the life, metabolism and activities of that insect. Kirkpatrick

(1923) has done the same with regard to the cotton-seed bug, *Oxycarenus hyalinipennis*, Costa, and the data that he obtained enabled him to evaluate the controlling influence of these two factors in nature. Exhaustive studies have also been made on the physiological life-history of the codling moth by Glenn (1922) and Shelford (1927, 1929). Both these authors studied the insect under controlled experimental conditions for a large number of years. The results enabled Shelford to construct charts showing the mortality in different stages and to calculate tables of the velocity of development at different combinations of temperature and humidity, with intervals of 0·5° of the former and 2% of the latter. For the methods of constructing charts and tables and for the discussion of the numerous details of the experimental work Shelford's papers should be consulted in the original (see also pp. 83, 85).

From the more general point of view it is interesting to quote Shelford's (1929) suggestion based on his unique experience with the codling moth, as to the comprehensive planning of experimental studies on physiological life-history. Such experiments should include the following series : (*a*) constant temperature experiments at 2–5° intervals, from 5° to 39°, with the humidities 45–100% at 10% intervals ; (*b*) variable temperature experiments, with temperatures and humidities within the limits of possible weather conditions ; (*c*) outdoor observations. "Such a programme of experiments requires 6000 to 10,000 individuals in each life-history stage and several men to carry on the work. The experiments should be repeated during each of two or three years, if possible." Since studies of this kind are arranged with a purely practical end in view, viz. to ascertain the controlling factors of a pest and to obtain data for practical forecasting, it appears highly doubtful that it will ever be possible to carry out such a comprehensive programme of work. Indeed, it is not certain whether results equally valuable, or, at any rate, sufficiently exact for practical purposes, cannot be reached by simpler and less costly methods. This end can be achieved by judiciously selecting, on the basis of some preliminary experiments, only such factors, and degrees of factors, as are most likely to be of the greatest practical value in a particular case. Janisch (1930) for example, in his work on *Prodenia litura*, F., studied only the influence of temperature, since other factors of the natural environment of this insect, particularly humidity, appeared to be of little controlling value. Similar partial work has been carried out with regard to a number of insects by various investigators and the value of the data obtained, though not constituting complete physiological life-histories, is in many cases sufficient for the estimation of the influence of the actual environment in the field.

The choice of factors to be tested in physiological studies on pests must be based on a knowledge of the conditions to which the insect is subjected in its normal environment.

(ii) *Climatic observations.*

It is a common practice amongst economic entomologists to judge the environmental conditions of an insect by the standard weather data supplied by the nearest meteorological station. These data, however, bear only a very distant and indirect relation to the ecoclimate and the microclimate of the actual habitat of the insect (see pp. 129, 131). In the first place, standard meteorological observations are taken in screens, *i.e.* in an artificial microclimate. Further, the calculation of mean values from the extremes only, the reduction of certain data to the sea-level, and other methods, designed by meteorologists for the purpose of eliminating purely local and incidental variations in climatic factors, tend to make the standard data of very little use to an ecologist. Moreover, there are a number of observations of the greatest importance from the ecological point of view, but which are not made by meteorological stations. Meteorologists may be prepared to introduce into their programmes some of the observations required by ecologists, but it is difficult to indicate to them exactly what observations of sufficiently general character are required. When climatic studies by ecologists can show that certain standardised observations are required, there is no doubt that meteorologists will be prepared to consider their general introduction.

It is, however, apparent, that the climate as observed in a meteorological screen and the ecoclimate, or the microclimate, of a habitat are not unrelated phenomena, since both depend on the same meteorological events. The dependence is in both cases indirect, but the interrelations between, for example, the temperature in a screen, and that in a standing crop should be more or less constant. In other words, it should be possible to arrive empirically at some formulae which would permit the calculation of, *e.g.*, the temperature in the standing crop, or inside a tree of a definite kind and size, from the air temperature as observed in the screen or from the readings of a thermometer exposed to the sun. This idea was put forward in my paper (Uvarov, 1929), read at the Conference of Empire Meteorologists in London (1929), and a corresponding resolution urging the necessity of research work in this direction was adopted. It is to be hoped that investigations in this direction will be initiated before long.

In the meanwhile, an ecologist has either to use the standard meteorological data, which in any case have a very definite relative value, or to make his own observations in the habitat of the insect. This latter course has the drawback that such observations cannot be utilised directly in other areas unless they are repeated there under exactly similar conditions. On the whole, however, ecoclimatic and microclimatic studies are unquestionably the best way of correctly evaluating and understanding the environmental factors of insect life.

It is not proposed to describe here the apparatus and the methods of observation used, or recommended for use, in such studies, as the subject has been recently dealt with by several authors (*e.g.* by Shelford, 1929; C. Townsend, 1924, 1926; Bates and Zon, 1922; R. Geiger, 1927; Friedrichs, 1930; Cutright, 1927; Hartzell, 1919).

(iii) *Analysis of meteorological data.*

Shelford (1920) was apparently the first to apply to ecological studies on insects the Ball-Taylor graphical method of representing weather or climate, though Sacharov (1925) adopted the same method quite independently. The method consists of plotting the mean temperature and the mean relative humidity for each month on the two ordinates and of joining the points by a line in the order of the months. The resulting chart is usually called a climograph, but it is scarcely worth while to sacrifice grammar in order to gain a syllable, and the term *climatograph* is to be preferred (Friedrichs, 1930*a*, introduced the corresponding German term, *klimatogramme*).

A *hythergraph* is a variation of a climatograph. In its preparation, the temperature and precipitation, instead of the temperature and humidity, are utilised (Fig. 50, top). The combined data of the temperature and precipitation are termed by Tehon (1928) *thermohyets*, and if one adopts this term, one can speak of thermohyetic conditions, instead of the cumbersome expression " temperature-precipitation conditions."

The same principle of plotting two factors may be conveniently used in several combinations (Tehon, 1928). For example, the mean thermohyetic conditions for a series of years in one locality, or for a series of localities, can be plotted together with the degree of abundance of an insect, so that a hythergraph is obtained showing clearly the conditions regulating abundance (see Fig. 51).

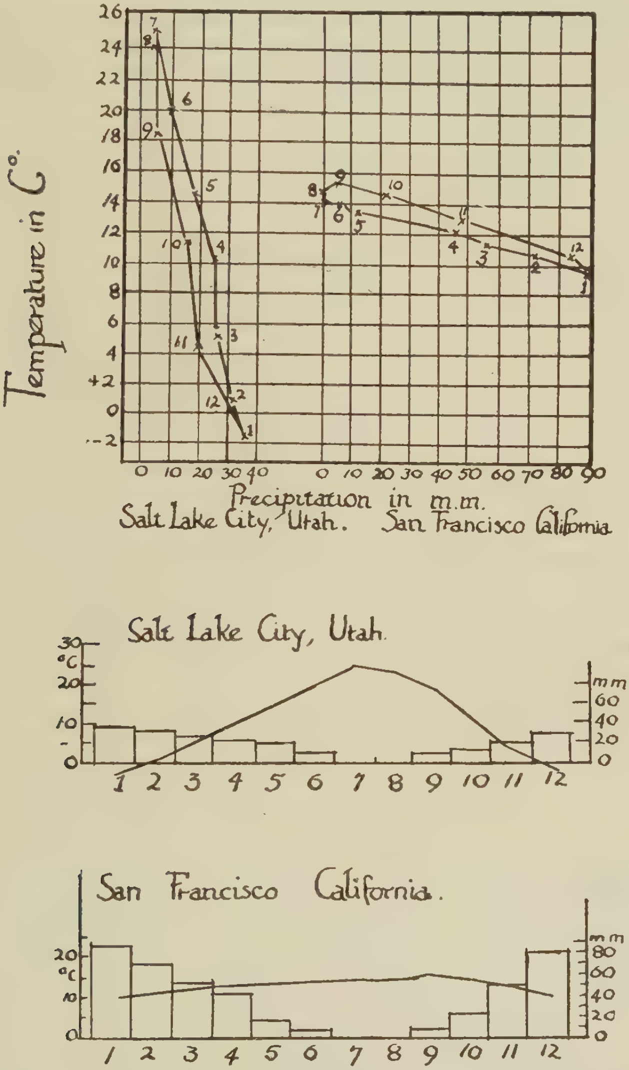

Fig. 50.—The representation of the climate of two localities by the usual climatographs (top figure) and by Bremer's method (two lower figures). (Redrawn after Friedrichs, 1930.)

Climatographs, or hythergraphs, may be drawn for certain seasons only. They may be based not on the mean, but on the extreme deviations, or on the range. Other meteorological factors, such as wind velocity, or vapour pressure can be used in various combinations, etc. In other words, there is an almost unlimited scope for the variations suitable for any particular ecological problem.

Bremer (1928*a*) suggested a modified form of hythergraph, in which the ordinate serves for months, the left abscissa for the temperature and the right abscissa for the precipitation (see Fig. 50, two lower figures). There is no doubt that this type of graph is much clearer, at least for the usual representation of thermohyetic conditions throughout a year.

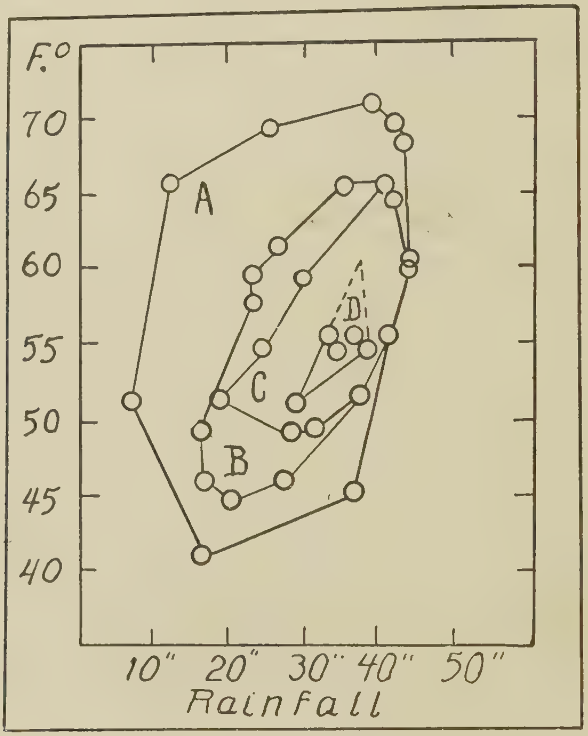

Fig. 51.—Mean annual thermohyetic ranges under which various intensities of cucurbit wilt develop. In the region marked A the wilt occurs in lightest form; in B it is mild; in C destructive; in D severely destructive. (After Tehon, 1928.)

(iv) *Quantitative studies on insect abundance.*

Studies on the fluctuations in numbers of insect pests are possible only by the adoption of a definite quantitative method, which enables the investigator to follow the gradation of the species in question, as well as of its natural enemies from month to month, and from year to year. For this purpose standard methods of collecting must be adopted. They are not described here, since this is a general problem of ecological technique and one which cannot be treated in a few pages (a brief summary of the quantitative methods for studying biocoenoses has been presented by Friedrichs, 1930; see also Börner, Blunck, Speyer and Dampf, 1921; Bremer, 1926*a*; Cook, 1928*a*; Arkhangelskiĭ, 1926; Dogel, 1924; Wladimirsky, 1926; K. King, 1929; Zubareva, 1930).

Quantitative studies on one pest, or on the whole population of a certain kind of cultivated plant, for a series of years, or in a series of localities, carried out side by side with climatic (preferably, ecoclimatic, or microclimatic) observations would make it possible to draw certain conclusions with regard to the possible climatic causes of fluctuations in the numbers of insects.

(v) *Correlation of climatic studies with quantitative data.*

Very satisfactory results can be obtained by a simple comparison of climatic data with the relative abundance of the insect studied in several localities, or in several years. Indeed, most of the work on the climatic control of the abundance of various pests has been done in this way. The introduction of climatographs and of hythergraphs has made the comparison very much easier. Indeed, there is even a danger that this method owing to its apparent simplicity may sometimes be misapplied (the work by Graf, 1925, and criticism by Sweetman, 1929; see p. 130).

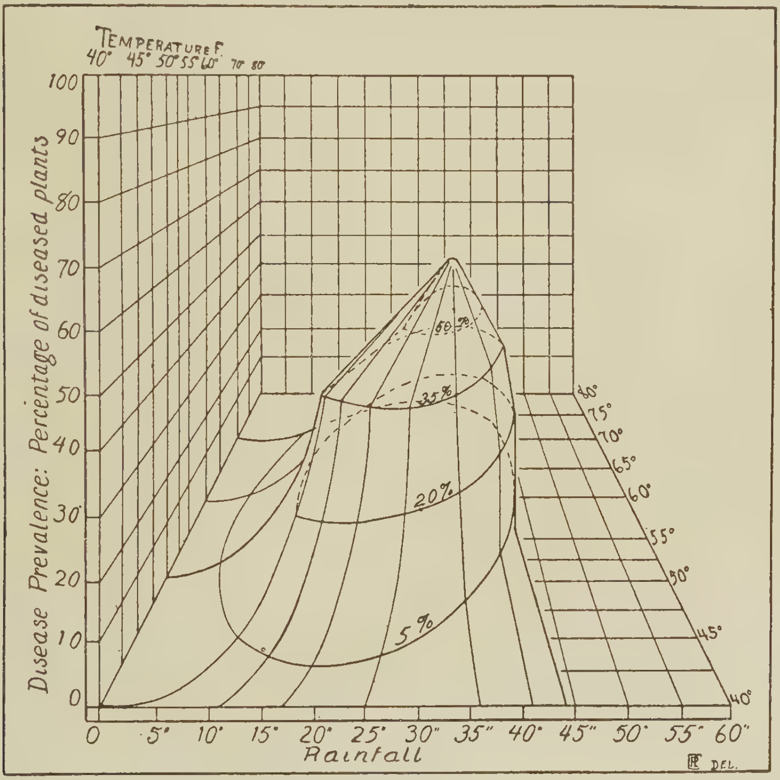

FIG. 52.—Three-dimensional graph indicating the interrelation of annual mean temperature, totals of annual rainfall, and the severity of pest attack. (After Tehon, 1928.)

While discussing the application of hythergraphs to the study of climatic factors of plant diseases Tehon (1928) reached the conclusion that the interrelations can be best expressed by a three-dimensional graph, in which the temperature and precipitation correspond to the length and the width of the base, while the severity of the attack is plotted vertically (Fig. 52). The idea is very interesting, but the practical application of a graph of this type must be limited.

In order to reach as objective conclusions as possible, Cook (1921, 1928*b*) and Kincer (1928) applied the statistical method of calculating partial multiple correlation to studies on insect abundance as regulated by climatic factors. By this method (see Yule, *An Introduction to the Theory of Statistics*, London, 1919) the relative value of each factor is mathematically brought out. Cook, however, was not satisfied that the method of partial correlation is the best one possible for determining the relative values, but, in his opinion, it at least represents a considerable advance over the method of estimating the relationships by inspection of a graph. This point of view may be correct, but a blind faith in statistical methods is dangerous, particularly when one deals with exceedingly complex cases of the interrelations of living organisms, or biocoenoses, and environmental factors. There is no reason why ecologists should treat statistical methods with more respect than statisticians. In this connection Yule (*l.c.*) make the following observations :

> " 'You can prove anything by statistics' is a common gibe. Its contrary is more nearly true—you can never prove anything by statistics. The statistician is dealing with most complex cases of multiple causation. He may show that the facts are in accordance with this hypothesis or that. But it is quite another thing to show that all other possible hypotheses are excluded, and that the facts do not admit of any other interpretation than the particular one he may have in mind."

The danger of statistical (and generally of mathematical) methods in ecology is that their application gives a stamp of extreme exactitude and reliability to conclusions even if derived from faulty, though sufficiently numerous, data. Once the method is mastered, the work of drawing conclusions from facts becomes mainly a mechanical process, instead of one of reasoning on biological lines.

It is practically impossible to obtain exact numerical data in quantitative ecological work, and all figures are either approximate, or represent the mean of more or less inexact figures. No mathematical treatment can render the basic figures more exact than they are, so that no conclusions drawn by the application of mathematical methods can be more convincing than those arrived at by a critical discussion of the data. Mathematical methods should be used in ecology, perhaps, more widely than they are to-day, but it must never be forgotten that they have their limitations and may even be positively misleading.

(*d*) **Forecasting.**

The economic entomologists of the present day are mainly historians of insect pests, in so far as they record and describe their outbreaks, and sometimes attempt to analyse their causes. They are, however, also expected to be prophets and to forecast the seasonal appearance of pests, the years of outbreaks and the ability of an introduced pest to survive in a new country. This can be done only on the basis of a most intimate knowledge of the pest and of its relations to its environment, *i.e.* of a thorough understanding of the whole bewildering complex of environmental factors and of the responses thereto of the insect. We have seen in the preceding sections how limited and fragmentary is our knowledge on these points. It is not surprising, therefore, that it is only quite recently that the first, almost timid, attempts at entomological forecasting were made. These are reviewed in the following pages, and it will be seen that, though the results actually attained are as yet very modest, the outlook for the future is promising.

The basis for entomological forecasting of any kind is the physiological life-history of the pest and the climatic conditions of the area, or the season, though some successful work in this direction has been done even without exhaustive physiological studies. The main data which should be known for forecasting are the limiting values of the climatic factors (see p. 120) and the influence of the latter on the rate of development (see pp. 19, 72) and on the abundance of the insect studied (see p. 136).

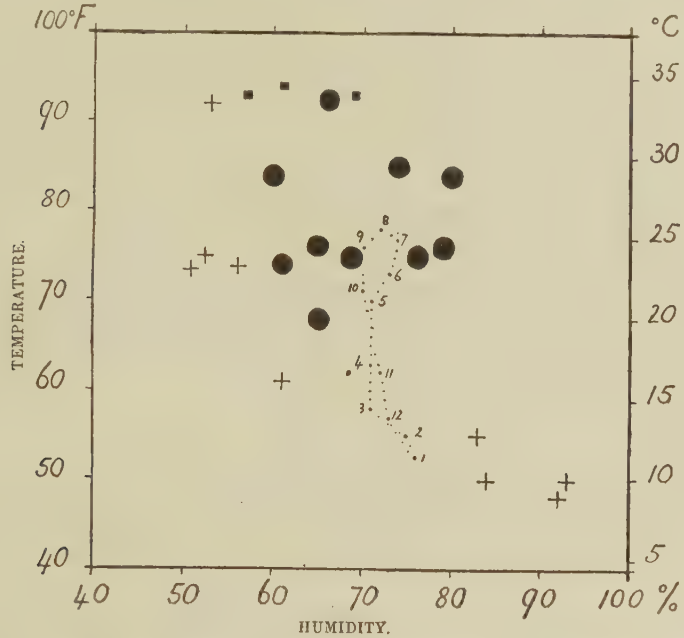

FIG. 53.—Graph showing the conditions of temperature and humidity which are favourable and unfavourable for the survival of rat fleas. Black circles signify more than 50 per cent. of survivals; a square signifies less than 50 per cent. of survivals; a cross, mortality of 100 per cent., or nearly so (data derived from Bacot, 1914). The dotted line is a climatograph for Jaffa, Palestine. It will be seen that the favourable area of the graph is fairly well defined and that the climate of Jaffa falls within that area for the summer months, but quite outside it for the winter months. (After Buxton, 1923.)

(i) *Forecasting of distribution.*

One of the first attempts at entomological forecasting was that of Gill (1921), in which he defined the areas where malarial epidemics are possible. On the basis of the temperature and humidity factors limiting the distribution of mosquitos and necessary for the development of the malarial parasite, he concluded that the meteorological conditions of a large part of England and Wales, and of the whole of Scotland and Ireland are definitely unfavourable to the transmission of malaria by mosquitos.

An outbreak of bubonic plague in Jaffa caused Buxton (1923) to analyse the local climatic conditions in relation to the survival of the eggs and larvae of fleas, by constructing a climatograph (Fig. 53) which proved that the climate of Jaffa may be favourable to fleas in summer but not in winter.

Mansfield (1924) analysed the climatic conditions of the areas of distribution of the Colorado potato beetle in North America and those in Germany, and reached the conclusion that the German type of climate is probably not wholly suitable to the pest.

A series of papers dealing with the forecasting of distribution has been written by Cook (1924, 1925, 1928, 1929), who based his work not on physiological studies of insects, but on actual observations of their relative abundance in different years and different areas and on parallel studies of the meteorological data represented by hythergraphs. The following example will make this method clear.

The pale Western cutworm, *Porosagrotis orthogonia*, Morr., was very injurious in Montana during the period 1915–1920, and the data on the damage (percentage of crops destroyed), on the monthly mean temperatures and monthly mean totals of precipitation for all meteorological stations within the infested area (including the stations where no damage occurred), were obtained. From the climatic data, and by weighting each entry with figures representing the percentage of damage at the respective station, computations were made of the monthly means of temperature and rainfall side by side with the means for non-infested stations (see Table XXXIX).

TABLE XXXIX.

Climatic Constants and their Differences for the Stations Infested and not Infested by Cutworms. (After Cook.)

	Temperature (F.°).			Precipitation (inches).		
	Cutworm stations.	All stations.	Difference.	Cutworm stations.	All stations.	Difference.
July	69·2	68·4	0·8	1·48	1·48	−0·43
August	67·0	66·7	0·3	1·00	1·06	−0·06
September	55·7	55·5	0·2	1·00	1·35	−0·35
October	42·8	44·4	−1·6	1·07	0·85	0·22
November	28·3	32·0	−3·7	0·47	0·57	−0·10
December	22·6	22·4	−0·2	0·45	0·54	−0·09
January	25·0	23·2	1·8	0·44	0·38	0·06
February	24·1	20·7	3·4	0·50	0·51	−0·01
March	28·4	30·6	−2·2	0·69	0·73	−0·04
April	40·2	40·3	−0·1	1·46	1·21	0·25
May	51·0	51·5	−0·5	1·54	1·89	−0·35
June	61·9	63·6	− ·17	1·52	1·79	−0·27
Annual (mean and total)	43·0	43·3		11·19	12·36	

The data for the infested stations served to construct a hythergraph representing the optimum conditions for the insect (Fig. 37, p. 123). This optimum hythergraph showed a semi-arid condition throughout the year, with moderate rainfall in each of the three spring months. The summer was hot and dry, and the autumn drier than the spring. The snowfall during the entire winter was light.

The next step was to compare the hythergraphs for various stations with the optimum hythergraph, and, by noting the resemblances and differences, to determine whether the station is suitable for the insect to become abundant. On the basis of these comparisons a map was constructed (Fig. 38) showing the areas where the Pale Western cutworm can be " normally present," " occasionally present," or " absent " as a pest though occurring as a species.

An examination of all the available records of the outbreaks of the cutworm was then undertaken, and none have been found outside the zone of possible occurrence, while all major outbreaks were confined to the inner zone.

Similar work on purely climatological lines has been done by Cook (1929) on the army worm, *Cirphis unipuncta*, Haw., and on the alfalfa weevil, *Phytonomus posticus*, Gyll. (Cook, 1925). In both cases maps were constructed on the basis of hythergraphs, and the actual records of economic distribution were found to agree closely with the maps.

In contrast with Cook's work, that of Bodenheimer (1925) on the Mediterranean fruit-fly, *Ceratitis capitata*, Wied., was based primarily on physiological data for the insect. An equilateral hyperbola derived from Blunck's formula (see p. 25) of the thermal constant was constructed on the bases of the experimental data on the length of development at different temperatures. This curve, and the mean annual temperatures made it possible to calculate the possible number of annual generations in any given locality. As a result, it was possible to classify the countries where the fruit-fly occurs as follows :—

(1) Countries where a permanent acclimatisation is impossible, since the number of days in a year with effective temperatures is not sufficient for a single generation to develop. Example : England.

(2) Countries where *C. capitata* is established permanently but the continuity of generations is interrupted by winter, when the development of a single generation takes about 110 days. Examples : The Mediterranean region, the cooler parts of Australia, California.

(3) Countries where generations follow each other continuously, the average temperature never being below 13·5°. To this class belong the tropical regions.

The data derived from the hyperbola were then tested by comparing them with the number of generations actually developing in the different areas of Palestine, where the local climatic conditions vary considerably. It was found that in every case the actual number of generations agreed with that calculated. Since the number of annual generations in the case of the fruit-fly is an index to the degree of its economic importance, the method has proved to be of value in determining the areas of economic distribution.

Work on the same lines has been done by Bodenheimer on a number of insects transmitting diseases (1925*a*), on two species of *Sitophilus* (1927), and on *Sitotroga cerealella* (1926).

A very interesting and promising, though little studied method of determining areas suitable for a certain insect is the *phytometer* method (Clements, 1920; Clements and Goldsmith, 1924; additional references will be found in these two fundamental books). This method is based on the idea that

> " every plant is a measure of the conditions under which it grows. To this extent it is an index of soil and climate, and consequently an indicator of the behaviour of other plants and of animals in the same spot."

The use of plants as indicators of certain conditions of soil and climate is, of course, not new, since the zonation of plant associations is commonly correlated with soil and climate. Similarly, ecoclimatic conditions can be judged by the presence, or absence, of certain plants.

Clements, as a botanist, developed the phytometer method for the study of the ecology of plants only, although his general definition quoted above suggests the possibility of using plants in studies of animal ecology. He even suggested, though in a very general way, that certain animals can also be used for the same purpose as *zoometers.*

A practical application of the phytometer idea to the ecological study of insects was made independently by Vinokurov, who used it in his work on the ecological distribution of grasshoppers in Siberia (Vinokurov and Rubtsov, 1930). Analyses of a number of plant associations were made, parallel with the study of their grasshopper population, and coefficients of common occurrence of certain species of plants and of grasshoppers were calculated. In this way, plant indicators for the occurrence of each grasshopper species were determined. Since grasshoppers do not depend directly on their plant indicators, the connection must be purely environmental, and, most probably, ecoclimatic, so that a plant may be utilised in this way as an indicator of an ecoclimate suitable for a species of insect. Further work in this direction should be very interesting.

(ii) *Forecasting of outbreaks.*

General considerations on the question of whether certain types of weather are favourable to a given pest have been expressed by many authors, but there are very few definite attempts at forecasting outbreaks on the basis of weather conditions.

The problem is certainly a very complex one, as has been pointed out by Stear (1928) and by Hinds (1928). Its study in each particular case involves quantitative work on the pest, studies of its physiological life-history, and an exact evaluation of the meteorological conditions and of their influence on the insect. The main difficulty lies, of course, in the fact that it has to be done some time before the beginning of the outbreak. This requires a theoretical evaluation of meteorological factors some time ahead, which amounts largely to guesswork, since the long-range forecasting of weather is still unreliable. However, with regard to many insect pests of temperate regions, the number of individuals entering hibernation bears a more or less definite relation to the number surviving the winter. Thus, the conditions of one year determine, to some extent, the probability of an outbreak during the next.

For example, the conditions favourable for an outbreak of the nun-moth have been defined by Sedlaczek (1915, 1916) as follows. The eggs, which hibernate from September to April, are very resistant to weather conditions. Winter weather has therefore no influence on the abundance of the insect. The development of larvae and pupae continues through May, June and July, and requires an accumulation of about 1500° of effective temperatures. In a warm summer the development is accomplished more rapidly, and the difference in the time of the emergence of the moths may amount to a month. The copulation flights of moths are possible only during still and rainless evenings with air temperature above 15°. The number of such evenings after the emergence of the moths and until the autumn depends on the time of their emergence. When there are more than twelve such evenings, the year is favourable for an increase and a gradation may be expected to begin in the following year.

Cook (1926, 1928*b*) applied the method of analysing weather conditions by means of hythergraphs to forecasting outbreaks of the pale Western cutworm, *Porosagrotis orthogonia*, Morr. Studies of hythergraphs for a series of years showed that the main factor in the abundance of the insect is the rainfall in spring and summer (May to August) of the year preceding the outbreak, the critical amount of the precipitation being between four and five inches. When it was over five inches, the cutworms decreased in the following year. When it was under four inches, an increase usually followed. Thus it is possible to predict the probability of an outbreak from the rainfall data of the preceding spring and summer. Essentially the same idea has been expressed by Seamans (1923) with regard to this species of cutworm. A few other examples can be found in entomological literature in which the study of conditions preceding an outbreak has made it possible to formulate conclusions as to its causes. These conclusions may often serve as a basis for forecasting outbreaks. So far, however, there has never been any actual forecasting, apart from the warnings issued by local entomologists based on the actual abundance of a pest. The first step towards organised forecasting may be seen in the annual surveys of the abundance of insect pests parallel with the meteorological conditions. This service is particularly well organised in the United States (Hyslop, 1922), where the weather data for each year are tabulated, presented graphically, and correlated with the insect outbreaks. In the temperature and precipitation studies departures from the normal, instead of the mean, are used, since acute outbreaks are considered as reflecting abnormal meteorological conditions. An arbitrary year is adopted starting with September, since insect outbreaks are considered as predetermined by the conditions prevailing during the late autumn and the early winter of the year preceding the actual outbreak and culminating before the end of the calendar year in which the outbreak occurs. Presumably a large amount of valuable data has been accumulated in this way, but so far this material has not been made public.

In England annual fluctuations in the abundance of the more common pests are recorded in the reports of the Ministry of Agriculture (Fryer, 1928), but no attempt is made to correlate these fluctuations with meteorological conditions, or to utilise the data for forecasting.

The collection of statistical data on the abundance of insect pests is particularly well organised in Germany, where since 1893 this work has been centralised in the "Sonderausschuss für Pflanzenschutz der Deutschen Landwirtschafts-Gesellschaft" (special section of the German Agricultural Society), but it is only quite recently that the enormous mass of data accumulated for the period have been summarised by Schnauer (1929). This author has presented a general survey of the course of the outbreaks of the main pests, viz. *Blitophaga* spp. (sugar-beet beetles), *Chlorops pumilionis*, Bjerk., *Jassus sexnotatus*, Fall., and *Hylemyia coarctata*, Fall. Apart from the data collected by the Agricultural Society, he has made use also of the entomological literature, agricultural reports, crop statistics, etc. The distribution of each species by years and by areas is given in a series of maps, while graphs representing the fluctuations in numbers from year to year are accompanied by diagrams showing the course of the main meteorological factors. With regard to each of the species treated, it was found possible to elucidate the probable connection of the outbreaks with a definite type of weather condition, and this conclusion can be used as a basis for forecasting in future. (Schnauer's paper contains a very extensive bibliography of the pests in question, as well as of the meteorological aspects of insect outbreaks generally and it should be consulted in the original.)

(iii) *Forecasting of seasonal events.*

The definition of areas suitable, or unsuitable, for a pest, and the forecasting of coming outbreaks are extremely important practical problems, but they do not arise as regularly as does the forecasting of the seasonal appearance of pests. Modern economic entomology includes a number of control measures which, in order to be effective, should be applied just before the appearance of the injurious stage. This involves continuous observations on the course of the development of the pest under natural conditions, but this is often not practically possible for an agriculturist who does not notice the pest until the damage is done. In practice, therefore, it is customary to recommend the application of certain control measures at more or less definite dates, and calendars of control measures in orchards, etc., are published for the guidance of agriculturists. It is scarcely necessary to point out that this practice is fundamentally wrong.

The realisation of the impossibility of correlating natural events with calendar dates has suggested to practical entomologists the idea of a *phenological* method, and control calendars have been evolved in which the times of the application of control measures are determined by some conspicuous events in the development of the host plant, *e.g.* the bursting of buds, the end of flowering, leaf-fall, etc. A typical example of this method is offered by the usual recommendation to spray apple trees against the codling moth immediately after the petals have fallen and before the calyx cups are closed. There is no doubt that the use of plants as indicators of the seasonal development of an insect may be carried much farther than is the practice at present (this point of view was strongly advocated, *e.g.* by Hopkins, 1918, and by Filipjev, 1928), but the problem has never been investigated in a sufficiently broad aspect. It must be realised that the plant most suitable as an indicator for an insect need not necessarily be its food-plant. Very careful and prolonged phenological observations on the insect and all plants usually occurring in its habitat are necessary to find the plant with the seasonal cycle most closely correlated with that of the insect. It must be always borne in mind, however, that the responses of every organism to external conditions are an integral part of its specific, and often its racial, characteristics, and no two organisms can be expected to respond to changes in all factors in exactly the same way. While, therefore, the flowering, for example, of a certain plant may normally coincide with the emergence of a certain insect, abnormal weather may in any given season affect the two organisms in a different way, in which case there will be a discrepancy in their development.

The *ecoclimatic* method of seasonal forecasting appears more reliable, at least on theoretical grounds, than those reviewed above. This is a term which may be conveniently applied to the method based on the physiological life-history of the insect, on one hand, and on the actual seasonal course of the weather, on the other. This method was originally suggested by the idea of the thermal constant for development (see p. 22). If the time necessary for the insect to complete a stage in its development depends on the accumulation of a definite amount of heat energy, as expressed by the sum of effective degrees of temperature, the actual observations on the temperatures from the beginning of the stage would show when that sum is approaching the constant, and when the stage may be supposed to be near its end.

The idea of the thermal constant, or of a constant sum of the effective day-degrees, has been used successfully by Glenn (1922, 1922*a*, 1922*b*; also Headlee,

1928) for forecasting the times of the appearance of various generations of the codling moth and for spraying against them. Experimental work carried out through several seasons enabled Glenn to estimate the average number of the effective day-degrees necessary to complete each stage. On the basis of these data a spraying calendar was prepared in which the time for the application of spraying against the larvae of each successive generation is indicated by the accumulation of the effective day-degrees. To compute the effective day-degrees, accurate thermograph records should be kept, and only the degrees above 10° taken into account. A correction must be introduced for temperatures above 30°, since they retard the development. Approximate determinations of the effective day-degrees may be made also from the maximum and minimum temperature according to a special formula.

Glenn's work has been continued by Shelford (1927), who introduced a number of important modifications and corrections. In his physiological investigations Shelford has taken into account not only the temperature, but all factors which may influence the duration of development, viz. variations in the temperature, humidity, etc. The investigations, partly described elsewhere (see p. 85), led to the evaluation of the rate of development at different conditions not in "day-degrees," but in developmental units (see p. 23). A total of 6480 developmental units was found to be necessary to complete the pupal stage, while 3864 units were necessary for the development of the eggs, and 18,000 units for the development of the larva. The practical procedure recommended for determining the times of spraying is as follows. The date of the first pupation of hibernating larvae kept out of doors, under conditions similar to those in the orchard, must be found by direct observation. From that date onwards, hygrothermograph records should be kept and the readings of the temperature and humidity for each hour should be tabulated. These readings should then be translated into developmental units, by means of a table showing the velocity values for each combination of temperature and humidity (see Table XL).

TABLE XL.

VELOCITY VALUES (NUMBER OF DEVELOPMENTAL UNITS PER HOUR) FOR VARIOUS TEMPERATURES AND HUMIDITIES, APPLICABLE TO THE PUPAE AND EGGS OF THE CODLING MOTH. (After Shelford; only a small section of the original table is reproduced here.)

F.°.	Per cent. humidity.									
	32.	34.	36.	38.	40.	42.	44.	46.	48.	50.
75° . .	22·1	22·1	22·2	22·3	22·3	22·4	22·5	22·6	22·7	22·8
74° . .	20·7	20·9	21·1	21·2	21·2	21·3	21·3	21·4	21·5	21·6
73° . .	19·7	19·9	20·1	20·2	20·4	20·5	20·6	20·6	20·7	20·8
72° . .	18·9	19·0	19·1	19·2	19·2	19·3	19·4	19·5	19·7	19·8
71° . .	18·0	18·1	18·2	18·3	18·4	18·5	18·6	18·7	18·9	19·0

Hourly values are then summarised, and when the sum approaches 6480 units, the time of the emergence of the moths may be predicted a week or more in advance (a correction may be necessary for the retardation or the acceleration of development caused by the autumn rainfall, and a special table is provided for the purpose). After this, if temperatures above 16·6° occur after sunset, the moths will begin laying eggs two days after emerging. From the date on which the first moth is estimated to have begun laying eggs, hygrothermograph records should be continued until 3864 developmental units are accumulated which will correspond to the hatching of the eggs. The time of the development of the larvae in apples is further estimated. It should take 18,000 units. The procedure is continued throughout the season for successive generations, so that the time of the appearance of each one can be predicted some days in advance.

It is unfortunately not known whether Shelford's method has ever been applied for practical forecasting, although an example from actual observations is analysed by means of the method, and practically all calculated times fall within a day or so of the actual event.

There is no doubt that Shelford's method of developmental units is theoretically well founded and very exact. It has, however, some very serious drawbacks. It should be realised that the preliminary work on the physiological life-history of the codling moth, necessary for the preparation of the table of velocity values, has taken ten years. This means that work on a similar scale has to be carried out in the case of each insect for which the basic data for practical forecasting are desired. Of course, some parts of the work on the codling moth were of a pioneer character, and the corresponding data for other insects can be now obtained in less time, but the programme of work on physiological life-histories, as outlined by Shelford himself (see p. 169), is still sufficiently formidable. Consequently, the method can be applied in practice only with regard to pests of exceptional economic importance, in the case of which an accurate forecasting is absolutely essential for control.

Further, the practical application of the method, when the table of velocities is prepared, is not devoid of serious difficulties. The keeping of hygrothermograph records and the calculation of hourly velocity values, with various corrections, would not commend itself favourably to an average fruit-grower. Moreover, the initial date of all computations, that of the pupation of the hibernating larvae, has to be determined by direct observation, and the probability of an error here is very great, while the whole season's forecasting depends on the accurate determination of this date.

All these considerations raise serious doubts as to the practical value of Shelford's method of seasonal forecasting.

An interesting example of the possibility of forecasting seasonal events in the life of a pest for the purpose of its control is offered by the work of Prinz (1928) on the larvae of *Polyphylla olivieri*, Zap., damaging roots of vine in Transcaucasia. In autumn the larvae burrow to a depth of 30–40 cm., when the soil temperature at 20 cm. reaches 10–12°, and move to the upper layers of the soil in spring at the same soil temperature (see p. 89). The use of carbon bisulphide against larvae is effective only when they are in the deeper layers of the soil. Collecting them by digging out is possible only when they are near the surface. Thus the knowledge of the soil temperature makes it possible to forecast the movements of the larvae and to determine the time for the application of one, or other, method of control. A similar connection was found by Prinz between the soil temperature and the seasonal movements of the vine *Phylloxera*. This knowledge again can be utilised for control.

(*e*) **The Utilisation of Climatic Factors for the Control of Pests.**

(i) *Phenological methods of control.*

Under this heading may be included the methods of controlling insect pests that aim at destroying the normal seasonal adjustment in the life-history of the pest and of its food-plant.

The best-known method of this kind is the control of the Hessian fly by the late sowing of winter wheat. This method is based on the fact that the life of an adult fly, which cannot feed, only lasts a few days. If the winter wheat is sown after the mass flight of the insect the crop will escape injury. The " fly-free " date can be established only by observations at an entomological station, and applies, of course, only to areas with the same climatic conditions. The necessity of making direct observations on the flight in every climatic area has been partly eliminated in the United States with the help of the, so-called, *bioclimatic law* developed by Hopkins (1918, 1919, 1921). This law, or, rather, this empirical rule, refers to the differences in the date of seasonal events according to latitude, longitude and altitude. The main clause of the rule is that " other conditions being equal, the variation in the time of occurrence of a given periodical event in life activity in temperate North America is at the general average rate of four days to each one degree of latitude, five degrees of longitude and 400 feet of altitude, later northward, eastward, and upward in the spring and early summer, and the reverse in late summer and autumn."

A map for North America was constructed showing the *isophanes*, that is, the theoretical lines along which all seasonal phenomena should occur at the same date, and this map can be used for the determination of the date of sowing winter wheat so as to escape infestation by the Hessian fly. Local conditions, however, cause considerable departures in the actual dates of seasonal events from those indicated by isophanes.

Znamenskiĭ (1924, 1925, 1926), in attempting to apply the bioclimatic law to conditions in Russia, had to introduce several important modifications. Instead of basing the isophanal map on degrees of latitude and longitude, he made use of the mean annual isotherms, and shifted the safe date of sowing four days later for each extra degree of the mean annual temperature. Another correction was introduced for precipitation, viz. for every 25 mm. of annual rainfall above the normal the date was shifted one day later.

Geissler (1927) found that climatic and phenological conditions of the European continent are such that an application of Hopkins' law to them is impracticable, and he suggested that, instead of the theoretical isophanes, maps of actual isophanes based on empirical data should be constructed.

The correlation between the stage of the development of maize at the time when eggs are laid by the corn-borer moths and the survival of the resulting larvae is very close (Huber, Neiswander and Salter, 1928). Therefore, an alteration in the date of planting, or the introduction of varieties developing at a different rate, presents a good phenological method of control. The principle of this method is, however, well known to every economic entomologist, since it has been recommended with regard to a number of insect pests, and there is no need to give other examples.

(ii) *Ecoclimatic methods of control.*

The cultural methods designed to alter unfavourably the climatic environment of a pest may be classified as ecoclimatic methods of control.

The fact that tsetse flies are very sensitive to air humidity suggested the idea of controlling their distribution by clearing infested forests so as to create conditions of temperature and evaporation unfavourable to the insects (Roubaud, 1909; Fiske, 1920; Swynnerton, 1921). This method is being studied at present in all its aspects by the recently established Tsetse Research Department in Tanganyika Territory (1929).

Essentially the same principle applies to the prevention of injury by borers in forests. For example, the injury by the white-pine weevil, *Pissodes strobi*, Peck., is invariably greater in open pure stands of white pine growing in full sunlight. In mixed stands, where hardwoods shade the pine, the injury is much less and decreases inversely with the intensity of shade until it reaches the zero point under a shade corresponding to that cast by an average stand of oak or maple. It is recommended, therefore, that white pine should be grown under a shelter-wood system that will provide a light shade for the young trees (Graham, 1926). A similar recommendation has been made for the prevention of attacks by *Cyllene robiniae*, Forst., on locust trees (Craighead, 1919).

The importance of the proper water balance in the food-plant for the insects feeding on it has been pointed out elsewhere, particularly with regard to bark-beetles (see p. 150), which develop best in trees having a water content below the normal. Craighead (1928) recorded that treatments aimed at increasing the water content of trees, such as defoliation (*i.e.* the reduction of the transpiration), or the supply of water to the roots, tend to check the development of bark-beetles and of the wood-staining fungi (*Ceratostomella*, sp.) associated with them.

Other examples of ecoclimatic and microclimatic methods of controlling insect pests can be found in the economic entomological literature, but the principle is sufficiently clear from the above cases. There is no doubt that, with the advance of knowledge regarding the ecoclimates and microclimates of insect habitats, methods of controlling insects by influencing their immediate climatic environment will be still further developed.

(iii) *Direct control by climatic factors.*

The use of radiant heat for the direct destruction of certain insects has been recommended more than once. Cunningham (1911) experimented with carpets infested with fleas and found that no live fleas remained after an exposure to sunlight for 60 minutes when the temperature under the carpet reached 27·8° and that over it was 29·5°. Reeves (1917) suggested controlling the alfalfa weevil by covering the surface of the field with something like a dust-mulch. On a bright hot day such a surface was heated by the sun to a degree sufficient to kill all stages of the pest. Craighead (1920) and Graham (1925, 1929) developed a method of controlling wood-borers in logs by exposing them to direct sunlight and turning them from time to time Patterson (1930) elaborated this method in great detail. Graham (1929) also recommended some methods of controlling borers in logs by a modification of the moisture content, *e.g.* by piling, barking and sun-curing, which reduce the water content, or by sprinkling the wood with water, or floating the logs, to increase the moisture content to a degree unfavourable for the pests. The possibilities of directly utilising climatic factors for the destruction of insects are very great, and the advantages of control methods in which the killing agency does not cost anything are obvious. It is to be hoped, therefore, that microclimatic investigations leading to such methods will find favour with economic entomologists.

Control methods which rely on the destruction of insects by high or low temperatures artificially produced do not come within the scope of the present work, and it will be sufficient to quote only some of the papers dealing with the subject, as follows :—

High temperature against insects in logs : Craighead and Loughborough, 1921 ; Graham, 1929 ; Snyder, 1923 ; Snyder and St. George, 1924 ; Welch, 1924 ; do., against grain, mill and household pests : Back and Duckett, 1918 ; Dean, 1911 ; Dean and Schenk, 1929 ; Gibson, 1916 ; Goodwin, 1914, 1922 ; Mills, 1836 ; Scott, Abbott and Dudley, 1918 ; do., against bedbugs : Gibson, 1918 ; Harned and Allen, 1925 ; W. Ross, 1916 ; E. Scott, Abbott and Dudley, 1918 ; do., against termites : Snyder, 1929 ; do., against the pink bollworm : Gough, 1916 ; Storey, 1916, 1917.

Low temperature : Back and Duckett, 1918 ; Back and Pemberton, 1916 ; Howard, 1896, 1897 ; Larson and Simmons, 1924 ; De Ong, 1921.

Vacuum : Back and Cotton, 1925.

Artificial light in orchards (apart from light traps, the literature on which is very voluminous) : Herms, 1929 ; D. Collins and Nixon, 1930.

(iv) *Effects of weather and climate on controlling insects by artificial methods.*

Weather conditions are a factor of outstanding importance in the application of a number of methods of chemical control.

Rains constitute one of the greatest obstacles to successful spraying with stomach poisons, through washing away the poison from plants and thus necessitating repeated spraying. Even a heavy dew has the same effect. Strong wind also affects spraying and dusting operations very unfavourably. The successful use of bait-traps and light-traps for catching moths is more dependent on weather conditions than is any other method, since the flight activities of moths are greatly affected by all weather factors. Poisoned bran baits for locusts and grasshoppers must be used with due regard to weather conditions, because the feeding on baits and the period during which the baits are effective depend on the temperature and humidity. The same applies to the control of locusts by barriers and trenches, since the behaviour of locust hoppers is an almost direct response to weather conditions. The method cannot be used, for example, in cool, or in very hot weather, when locust hoppers do not march and cannot be driven.

The toxicity to insects of stomach poisons and fumigants greatly depends on the temperature, as does that of contact insecticides (Shafer, 1915 ; Brinley and Baker, 1927). The possibility of injury to the foliage by sprays is also determined by weather conditions (Fernald and Bourne, 1922).

Meteorological factors are of exceptional importance in the biological control of pests, though it must be admitted that, so far, most of the work in connection with the introduction of the natural enemies of insect pests from one country into another has been, and still is, conducted without any serious attention to the climatic aspect of the problem. It is not known what percentage of the failures of introduced parasites to establish themselves in a new country is due to the climatic conditions being unsuitable. There is, however, one recent case of an unsuccessful attempt at biological control which has been well investigated climatically. I refer to the introduction into Egypt and Palestine of a Coccinellid, *Cryptolaemus montrouzieri*, Muls., for the control of the sugar-cane mealy-bug, *Pseudococcus sacchari*, Ckll. Nearly 250,000 beetles were introduced into Egypt in the course of seven years, but without any success. Hall (1926) explained this mainly on climatic grounds, and Bodenheimer and Guttfeld (1929) confirmed his conclusions with regard to Palestine, where the climate closely resembles that of Egypt and where an attempt has been made to introduce the same beetle for the control of the citrus mealy-bug, *Pseudococcus citri*, Risso. The last two authors have thoroughly investigated the problem by studying the physiological life-histories of both species under the actual climatic conditions of Palestine. The rate of development of both insects in different months, *i.e.* under different mean temperatures, was determined and the curves (hyperbolae) of development as dependent on the temperature were constructed. It was found that *Pseudococcus citri* in the coastal zone produces 7 to 8 annual generations, while *Cryptolaemus* has six. A study of the limiting factors proved that the beetle suffers greatly both in winter from cold and humidity, and in summer from the excessive heat and dryness. *Cryptolaemus* can only effectively control *Pseudococcus* with mean temperatures of about 18–23° for 3 to 5 months, which are never found either in Palestine or in Egypt. On the contrary, the same beetle proved to be able to establish itself in California and on the Riviera, where the climatic conditions are more favourable to it.

Bodenheimer and Guttfeld studied by the same method several native natural enemies of the citrus mealy-bug and found that the Hemerobiid, *Sympherobius amicus*, Navas, and a Cecidomyid are much better adjusted to the local climate than *Cryptolaemus*, and they are very effective as controls.

These investigations are of great general interest, since they prove the possibility of determining the chances of a predator or a parasite to establish itself when introduced into a new country, and of evaluating their probable controlling influence on the pest, by studying the physiological life-histories of the insects concerned in their relation to the actual climate of the country. The method deserves the serious attention of all entomologists and institutions engaged in biological control.

The practical necessity for similar bioclimatic studies in all cases of proposed introduction is made clear by the fact that the greatest percentage of successful introductions of parasites falls to Hawaii, a country where the monthly means of temperature and rainfall are practically the same throughout the year and no extremes of any factor occur. On the other hand, there are scarcely any cases of successful biological control in countries having a temperate climate and pronounced seasonal fluctuations in weather (Stellwaag, 1929*a*).

It is hardly necessary to quote examples illustrating the importance of weather conditions for the use of parasitic fungi in insect control. Wherever the practical utilisation of fungi for control has been attempted, it has been invariably found that no results can be obtained if the weather is unfavourable to the development of the fungus. On the other hand, suitable weather (abundant humidity and sufficiently high temperature) results in spontaneous epidemics, and the artificial dissemination of pathogenic fungi becomes unnecessary.

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THE EARLY STAGES AND BIONOMICS OF *TRICHOCERA MACULIPENNIS* (MEIG.) (DIPTERA, *TIPULIDAE*)

By K. R. Karandikar, M.Sc. (Bombay), Ph.D. (Edinburgh).

[Read 5th November, 1930.]

Plates I–IV.

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Introduction.

Trichocera maculipennis (Meig., 1818), according to Edwards (8, 13), has not been observed in Britain outside the Lowlands of Scotland and the English Lake District. This fact, along with the interesting and somewhat unusual habitat of the larva, suggested the working out of the bionomics of this species. The following paper contains a study of the life-cycle and habitat of *T. maculipennis*, together with structural descriptions of the early stages. The work was carried out during 1928–29 at the Entomological Laboratory of the University of Edinburgh under the supervision of Dr. R. Stewart McDougall, to whom I wish to acknowledge my sincere thanks. The material for the investigation was supplied by Mr. P. M. Innes, manager of the Cragganmore Distillery Works, Ballindalloch (Scotland), and Mr. C. McKenzie; to both these gentlemen I am greatly indebted for their frequent help.

Trichocera maculipennis is a Dipterous fly belonging to the Trichocerinae, which forms one of the sub-families of Tipulidae. Meigen (1818) was the first to find this species and named it *maculipennis* from its spotted wings. Since then, little or nothing seems to have been done regarding the bionomics or structure of *T. maculipennis*, although work has been done on other species.

It would not be out of place to state here the main features of the habitat of the genus *Trichocera* in general, as studied by various observers. Perris (1) was the first to describe the larva of *T. annulata*, with notes on its life-history and habitat. The larvae of this species, as Perris says, are found in the midst of decomposing vegetable matter; they live gregariously amongst rotten gourds and fungi of the *Agaricus* group. Perris further says that he found the fly to be very common during October, November and December at Mont-de-Marsau (South of France), upon hedges, manure, fungi, etc.

Others have recorded their observations on species of *Trichocera*, and among them Keilin. His paper (5) is much more recent and quite exhaustive. With regard to the distribution of *Trichocera*, Keilin says that they are common in all temperate regions, and that they are also found in cold regions. He also observed that adults of *Trichocera* appear just at the approach of autumn and during winter, and that they are found dancing in groups, especially in favourable weather. His observations on the habitat of *T. annulata*, *T. hiemalis* and *T. regelationis* show that the larvae of these species are found in certain decaying fungi or under dead leaves in gardens or places where organic matter exists in a state of decomposition. With regard to the habitat of *T. regelationis*, Rhynehart (9) wrote that the larvae are found amongst rotting swedes and decaying portions of their roots; and that the eggs are laid in the decaying tissues of the swedes.

From the foregoing details, it will be clear that species of *Trichocera* in general are found during autumn and winter, when most other flies are dead or hibernating; and that the *Trichocera* larvae are found feeding in decaying organic matter, that is, in habit they are scavengers. These statements will be of particular interest when later on I record my own observations on the habits, habitat and life-history of *T. maculipennis*.

HABITS AND HABITAT OF THE LARVA OF *T. MACULIPENNIS*.

During the spring of 1928 Mr. P. M. Innes of the Cragganmore Distillery sent a small tin box carrying some refuse from the distillery works. It contained a few clinkers covered with a slimy, dark-looking, odorous substance, moving about in which were a number of larvae. The latter were reared and the adults were identified as *T. maculipennis*.

In order to arrive at a clear idea of the habits and habitat of this larva it would be advisable to give here a short history of the origin of the distillery refuse which forms the breeding-place of this species. In the process of preparing the malt in the distillery, barley is soaked in water, and in the presence of other conditions for germination, the ferment secreted by the cells of the scutellum acts upon the endosperm, which is chiefly starch, and the latter is changed to sugar. It is this sugar that the distiller wants, and not young barley seedlings, and therefore, in due course, the germinating process is brought to an end. Cleaning follows to remove husks, etc., and then all is ground up into fine flour to which hot water is added. This malt, as it is called, is removed to a tank and yeast added, when fermentation follows. When the proper time has arrived, the alcohol is led off in one direction and the malt-yeast residue in another to a large open tank. Here much of the matter sinks to the bottom, and more or less solidifies to form a useful cattle-food. The water still containing impurities is led to another tank, pure water and lime being added. More solid matter settles down at the bottom, and this has some use as manure. What is left over is fed to a reservoir near which are situated the so-called "filters." The filters contain "clinkers" piled up to a height of 20 feet. Tubes lead the water with its impurities to these filters, where the impure water is sprinkled over the clinkers. Water filters down through the clinkers and is collected below in the basin running all round the base of the filters, and is drained ultimately into the river.

A slimy, dark-looking, semifluid matter, with a very unpleasant odour, remains behind attached to and coating the clinkers; and it is in this slimy residue of the distillery that the larvae of *T. maculipennis* were found in numbers. The larvae were voracious eaters and fed upon this waste odorous refuse.

When the distillery is in full working order, this slimy mass forms a thick layer over the clinkers; but it all soon disappears as a result of the scavenger habits of the *maculipennis* larvae.

The adults and the larvae of *T. maculipennis* were first observed by the manager of the distillery in spring 1925, and their presence was recorded till the middle of September of that year. Similar observations were made during 1926 and the subsequent years, and it has been found that the larvae of this species have been first observed at work about the middle of March every year. The adults begin to appear about the beginning of April and can be found till the end of September. From October till March adult *maculipennis* have not been observed, and an examination of the distillery refuse during this period has failed to indicate the presence of this species at any stage in the refuse.

While the larvae of *T. maculipennis* were easily the most abundant species, other Dipterous larvae were also present in the refuse, playing the same part of scavengers. For example, the larva of the common moth-fly of sewage works, *Psychoda severini*, was very common in the distillery residue.

LIFE-HISTORY.

In the first week of May 1928 I had the first opportunity of examining material of *Trichocera maculipennis*, sent from Cragganmore Distillery. Quite a number of larvae of this insect were found moving about in the slimy refuse. A few days later some of the larvae, having reached their fully-grown stage, were found pupating and a week or so later adults issued. I tried to breed out a new generation of this insect, in the Laboratory, by caging together male and female adults, but it was not very successful during that summer. Pairing took place in the breeding cages and eggs were laid upon the damp soil offered in the experimental cages, but none of the eggs hatched. From the successful breeding in the next year, one may suppose that the nidus for these 1928 eggs was unfavourable.

During 1929 the material came rather late in the month of July. About 25 larvae were found in the material, some of which pupated in time, and after a week adults began to emerge. I caged together males and females and after a few days the fertilised females laid eggs, and with these I was able to follow up the complete life-cycle of this fly, from egg to adult.

The various details are as follows :—An adult female appearing on 11th of August, 1929, was caged with a male that issued on 22nd of August, 1929. Special care was taken this time to offer, as far as possible, a natural surrounding for the fly to lay her eggs, and give favourable conditions for their subsequent development. For this purpose the ground surface of the cage was covered over with a thick layer of ordinary soil mixed with the slimy, odorous refuse from the Distillery. This was kept distinctly wet throughout the experiment, and throughout retained an appreciable odour.

Pairing took place, and on 26th of August the female began to show signs of sluggishness, with an inclination to walk over the surface of the damp soil in the cage rather than fly about. The next morning the female was noticed laying eggs, singly as well as in masses, on the wet soil. The mode of laying eggs was rather interesting. While walking over the surface of the prepared soil, the female would suddenly stop. The terminal portion of her abdomen, which, while she was walking, was obliquely inclined to the surface, became bent under on itself, so that the ovipositor was carried forward under the abdomen. The ovipositor then was suddenly thrust down in the soil. A minute passed in this position, and then suddenly the fly pressed herself to the ground and remained in this position for two minutes. During this time the egg was laid. The female then recovered her original position, straightened her abdomen and began to walk forward over the soil. The number of eggs laid by this female was about 40; the maximum number laid by another fertilised female was 124. The females died after laying their eggs.

The newly-laid egg (fig. 1) is elongated oval in shape, with a transparent shell enclosing the white contents. After five or six days the egg-shell broke by a vertical slit at its anterior end and the young larva hatched.

The newly-hatched larva (fig. 4) began at once to move about and feed. Consequently growth in size was rapid, and in 25 days the larva was full-grown and ready for pupation. Before it pupated the larva stopped feeding and became sluggish. Its body was noticed to be a little contracted. It then buried itself just beneath the surface of the soil. After a short quiescent stage the larva moulted and pupated. The moulted skin was often found attached to the hind end of the mummy-like pupa.

Normally the pupa is inactive, but if irritated or placed in uncongenial conditions, it exhibits wriggling movements of its body. When, for instance, the soil round about the pupa was dug up a wriggling movement of its body followed and attempts were made to avoid the light. Just before the emergence of the adult fly, the subterranean pupa, by means of the blunt backwardly directed spines on its body, pushed itself up through the moist soil and took up a position, with the head just above the surface of the soil. This position makes it easy for the emerging adult to escape safely from the pupal skin. The pupal life lasted from 7 to 9 days. When the adult was ready to emerge, a slit occurred along the mid-dorsal line of the pupal thorax; the adult fly slowly projected its head, and gradually the thorax and abdomen were freed; the legs were the last to free themselves from the pupal sheaths. The whole process from the breaking of the pupal slit to the complete emergence of the adult took not more than five minutes.

The following are some of the records bearing on the life-cycle of this fly :—

	I.	II.
Male and female caged together . .	Aug. 22, 1929	Aug. 24, 1929
Eggs laid	„ 27, 1929	„ 29, 1929
Preoviposition period . . .	5 days	5 days
Larvae hatched	Sept. 2, 1929	Sept. 3, 1929
Egg-stage period	6 days	5 days

The larval period on the average was 27 days; *e.g.* a larva which hatched on the 2nd of September, 1929, and was closely observed, pupated on the 29th of September in the temperature of the Laboratory.

Pupal Period.

	Date of Pupation.	Date of Adult Emergence.	No. of Days.	Sex.
(1)	28.5.28	4.6.28	7	♂
(2)	6.6.28	14.6.28	8	♂
(3)	2.7.29	10.7.29	8	♀
(4)	2.8.29	11.8.29	9	♀
(5)	11.8.29	19.8.29	8	♀
(6)	14.8.29	22.8.29	8	♂
(7)	17.8.29	24.8.29	7	♂

Length of life of the Adult Fly.

	Date of Emergence.	Date of Death.	Length of Life.	Sex.
(1)	6.6.28	19.6.28	13 days	♂
(2)	6.6.28	21.6.28	15 ,,	♀
(3)	6.6.28	23.6.28	17 ,,	♀
(4)	7.6.28	23.6.28	16 ,,	♂
(5)	11.7.29	21.7.29	10 ,,	♂
(6)	11.7.29	23.7.29	12 ,,	♂
(7)	11.8.29	27.8.29	16 ,,	♀
(8)	14.8.29	29.8.29	15 ,,	♀

From the above table the life-cycle of *Trichocera maculipennis*, from the time the egg is laid to the time the adult fly emerges, took about 40 to 42 days, under laboratory conditions, at an average temperature of 60° F. The egg-stage lasts from 5 to 6 days; the larva takes 25 to 30 days to complete its growth. The pupal stage extends over 7 to 9 days. The adults fed in the cages on honey and water lived from 10 to 17 days.

DESCRIPTION OF THE VARIOUS STAGES.

Egg.—The egg of *T. maculipennis* (fig. 1) is creamy white in colour, elongated oval in form, bluntly pointed at each end and thicker in the middle. The surface of the egg-shell is granular in appearance. Length of the egg is ·46 mm., breadth ·17 mm.

The various changes observed in the growth of the newly laid egg, before the newly formed larva hatched out, are as follows :—The egg contents of a newly laid egg, after about 20 hours, detach themselves from the two blunt ends of the egg-shell and collect towards the centre (fig. 2). After two days (fig. 3) the central mass is seen divided into two portions; an anterior smaller and round (a.p.), and a posterior larger and elongate (ps.p.). The smaller anterior portion begins to differentiate itself into the head region of the larva, while the larger posterior one develops into the body of the future larva. After five or six days, the newly formed larva hatches out by a vertical slit in the anterior region of the egg-shell.

Young Larva.—The newly hatched larva (fig. 4) measures about 1·27 mm. in length, and is brownish grey in colour. The larval structure known as the "egg-burster" present in the newly hatched larvae of some Diptera is not found in the case of *T. maculipennis.* The head of this larva, which is comparatively large, is not much chitinised. The chitin of the head, being therefore somewhat transparent, the pharynx and its working could be observed under the binocular microscope. The antennae (ant.) are easily noticeable, and so are the eye-spots (e.). The latter are situated at the sides of the antennae and are marked by the presence of red pigment. When examined under the high power of the microscope, the body of the early larva is seen coated with very fine hairs. The segmentation of the body is prominent, due to the presence of slightly chitinised brownish rings which occupy the intersegmental region. Secondary segmentation is also noticeable, but not to the same degree as in the case of the fully developed larva. Prothoracic spiracles are wanting. The hind pair of spiracles (h.sp.) borne by the last segment are situated between an upper and a lower pair of fleshy lobes (f.l.). The lobes are covered over with long fine hairs, except on their inner sides. The tracheal trunks, which can be traced from the hind spiracles, owing to their being visible through the transparent integument, run forward, one on each side of the body. The nervous system, together with its segmental arrangement of ganglia, can also be seen clearly through the chitin, and similarly one sees the alimentary canal with its pale-coloured contents.

FULLY DEVELOPED LARVA.

(a) *External Characters* :—

(i) *Body*.—A fully developed larva of *T. maculipennis* (fig. 5), stretched to its full length, measures 10 mm. in length, by 1·3 mm. in breadth. It is yellow-white in colour, and its body is slightly flattened dorso-ventrally. A free chitinous head region is followed by a body of 11 segments, there being little or no demarcation between thorax and abdomen. Each segment of the body is further divided into two or three pseudo-segments, owing to the presence of transverse folds. The first four segments of the body, behind the head, are divided each into two secondary segments; each of the next six is divided into three; and the last one into two secondary segments. The lateral margins of the body are wavy in form, owing to the secondary segmentation which is not limited to the dorsal surface of the body. The integument of the body, though thinly chitinised, is tough in consistency, and is covered with rows of fine hairs; a few stout bristles are scattered here and there.

The larva is legless, but under the microscope two clear spots are seen on the undersurface of each of the first three segments of the body behind the head (fig. 6). On each of these spots one finds four bristles, two of which are stouter and longer than the other two.

The first segment of the body—the prothoracic segment—bears a small spiracle (p.sp.) on each side dorso-laterally. The last segment of the larva (fig. 7) carries on its dorsal surface two pairs of fleshy lobes (f.l.) of which the posterior pair is longer and larger than the other. The inner faces of these lobes are formed of a layer of yellowish chitin, distinctly thicker than the surrounding chitinous integument. On their outer surfaces the lobes carry a series of long bristles disposed more or less like a fan. Between these lobes, nearer the base of the dorsal pair, are situated two spiracles (h.sp.) brownish black in colour and much bigger than the prothoracic pair. In the living condition, the so-called spiracular lobes (f.l.) were often noticed to close in towards each other and thus protect the spiracles, whenever the latter were exposed to the danger of being choked by the introduction of foreign material.

On the ventral side of the last segment of the larva lies a circular anal plate (figs. 8, 9, an.pl.) through which the anus opens to the exterior by means of a four-grooved anal aperture (an.gr.).

(ii) *Head* (figs. 10, 11).—The head of this larva, being free from the rest of the body, is partly retractible into the prothoracic segment. It has the form of a chitinous capsule broader at the hind end, and longer on the dorsal than on the ventral side. The posterior edge of this capsule is thickly chitinised. The position occupied by the clypeus (cly.) can be made out only by means of a faint incomplete suture lined by a row of spines on either side.

The mouth is situated ventrally. The mouth-parts are: a labrum (lbr.) and epipharynx (ep.) on the dorsal side and in front of the mouth; a pair of mandibles (md.) at the sides; below and behind these, a pair of maxillae (mx.) and ventrally the labium (lb.).

The labrum (figs. 10, 11, 12) is a prolongation of the clypeus. Anteriorly it merges into the epipharynx (ep.), which is bent ventrally. At the point of the bend there is a definite joint (j.) dividing the labrum proper from its ventrally curved epipharyngeal portion.

The epipharynx (ep.) is rather a complex structure. Figure 12 will help to explain it. It is somewhat round in form, and covered with hairs some of which are conspicuously bristle-like on either side of the median line. The median line shows also a few small papillae (pal.) which may be of a sensory nature (5). Apically the median line ends in a small blunt process (pr.), below which is situated another larger U-shaped prolongation (U.pr.) covered with stiff spines and papillae (pal.). At each side of this U-shaped prolongation is seen a chitinous dentate or comb-like structure (cmb.). The latter possesses six prominent teeth, and is continued below carrying a varying number of pointed spines.

The term " epipharynx " used in the above description is that used by Rhynehart (9) in his paper on *T. regelationis.* While describing the " comb-like " structure mentioned above, Rhynehart (9) found, in the case of the larva of *T. regelationis*, only six chitinous teeth in each comb. Keilin (5) in his description of the larva of *T. hiemalis*, does not record the exact number of teeth.

Mandibles (figs. 13, 14).—At the sides of the labrum, viewed from the dorsal side, are situated a pair of well-developed and strongly chitinised mandibles. Each mandible consists of two portions : a large proximal portion (p.p.) and a relatively small distal one (d.p.). The basal margin of the proximal portion is somewhat semicircular in outline and gives off a curved chitinous process (dr.cd.) on its dorsal side, termed the " dorsal condyle " by Rhynehart in *T. regelationis.* This dorsal condyle, by which the mandible is articulated to the cephalic capsule, serves as a hinge-like mechanism for the dorso-lateral movement of the mandible. The inner side of this proximal portion of the mandible (p.p.) has a concave depression (cn.d.) in which are present a bunch of long, fan-like hairs. The same depression gives attachment to the large adductor muscles (add.m.). A little in front of this concave pit, verging on the sides of the mouth, is seen a dentate chitinous structure (dt.st.) provided with one large tooth (t.) and five smaller ones. On the outer convex side of this proximal portion of the mandible there are two stout, many-branched bristles; an unbranched bristle is found on its ventral surface.

The distal portion of the mandible (d.p.) is deeply chitinised and strongly toothed. The teeth (t.), 7 to 8 in number, are arranged in a fan-like fashion, and curve somewhat inwards towards the mouth-aperture. The outer base of this distal dentate structure (d.p.) is lined with bunches of long, stout hairs.

Maxillae (figs. 11, 15).—Below and behind the mandibles are situated a pair of maxillae (mx.). Each maxilla is composed of a proximal portion (mx.p.p.), and a distal one (mx.d.p.). The proximal portion can be said to be homologous with fused cardo and stipes (9). It carries on its ventral surface bunches of long yellow-coloured hairs arranged in small transverse rows. Among them stands out one stout backwardly bent spine (spn.).

The distal portion of the maxilla is divided, by means of an incomplete vertical notch (v.nt.), into an outer portion homologous with the maxillary palp (mx.pl.) and an inner one bordering the mouth. The maxillary palp has on its ventral surface a conspicuous pit (sns.p.) containing about 16 sensory papillae. All around this pit the palp has a coating of fine hairs which are replaced by a few longer ones near the anterior margin. The inner portion of the maxilla (d.p.) bears two or three blunt tooth-like processes (t.). In addition to these, it also carries a few stout spines which point inwards towards the mouth-cavity. In amongst these spines are numerous shorter and longer hairs. A little outer to the maxillary teeth (t.), between them and the vertical notch (v. nt.), is seen a sensory area (sns.a.) carrying a few blunt sensory papillae surrounded by fine long hairs.

Rhynehart, (9) in his description of the larval mouth-parts of *T. regelationis*, found in the sensory area (sns.a.) described above, a homology with the "galea," while the teeth-bearing maxillary region mentioned above he likened to the "lacinia."

Labium (fig. 15).—The labium of *T. maculipennis* larva is less chitinised, and probably functions more as a sensory organ than aiding in mastication (5). On its outer surface are seen two prominent swellings: an anterior one (end.), and a posterior one (exo.), named the endolabium and the exolabium respectively (5). The endolabium bears small tufts of very minute hairs on its sloping surface. The exolabium also carries similar tufts of minute hairs, but in addition to these there are present 10 to 11 sensory papillae on its dome-like surface. The posterior part of the labium, which is fused to the proximal portion of the maxilla on either side, is covered over with bunches of long yellow-coloured hairs arranged in transverse rows.

In his description of the labial region of the larva of *T. regelationis*, Rhynehart (9) determined the exolabium of Keilin (5) as the labium proper, and Keilin's endolabium as the hypopharynx. Moreover, he found in one pair of the sensory papillae, described above as present on the exolabium, a homology with a reduced labial palp.

Antennae (fig. 16).—The antennae are situated in small circular pits in the dorsopleural region of the head-capsule, a little behind the base of the mandibles. Each antenna (ant.) consists of two parts: a basal joint (bs.j.) carrying a series of blunt sensory papillae (pal.), and a terminal one (t.j.) having the form of an inverted bell.

Eye (fig. 16).—In the neighbourhood of the antenna on each side are three transparent oblong dots (e.), arranged in a triangle and surrounded by a few stiff spines. They constitute the eye of this larva. It may be mentioned here that while a red pigment was noticeable in this eyespot of the early larva, no trace of red was visible in the case of the full-grown larva.

The *internal skeleton* of the head-capsule consists of a pair of chitinous rods which take their origin internally near the mandibular base and descend down backwards to articulate with the ventral posterior corners of the capsule.

(b) *Internal Structure* :—

Under a fairly tough cuticle the body-wall is formed mainly of longitudinal muscles grouped in definite bands. The body-cavity of the larva is filled with the fat-body arranged in two much-folded semi-cylindrical masses (fig. 17, f.ts.) which envelop the alimentary canal throughout its whole length.

The Digestive System (fig. 17).—The alimentary canal in this scavenger type of larva, when dissected out, measures a little longer than the body. It is divided into the fore-gut (f.g.), the mid-gut (m.g.) and the hind-gut (h.g.), and is provided with salivary glands (sl.gl.) and malpighian tubules (mlp.).

The mouth, which opens on the ventral face of the head-capsule, is formed by the labrum and epipharynx above and in front, the mandibles and maxillae at the sides and the labium below and behind. It leads into the chitinous pharynx (ph.), which presents a somewhat peculiar structure. Figures 18 and 19, will help to explain it. Looked at from the side (fig. 19), the pharynx suggests the shape of the upper portion of a funnel, with its stalk comparable to the oesophagus (oes.) issuing from it ventrally behind. Examined from the dorsal aspect (fig. 18), the inner sides of the pharynx, as in the case of the funnel, close in or narrow down towards the central cavity (oes.op.), which leads into the oesophagus. One also sees these inner sides of the pharynx lined with rows of fine hairs (r.h.) directed downwards towards the oesophageal opening. Internally, the pharynx on its dorsal side is covered over with a chitinous shield-like lining (figs. 12, 19, sh.l.), open in front where it is attached to the upperside of the mouth-cavity in front of the epipharynx. This shield-like cover is lined on its inner face with rows of fine hairs directed backwards. The pharynx is held in position and worked by means of muscles attached to the wall and to the internal skeleton of the head-capsule.

Following the pharynx comes the oesophagus (oes.), which has a chitinous lining and is supported near its origin by eight chitinous bands (cht.b.) running longitudinally along its wall. The oesophagus is continued behind as far as the metathoracic region, where it leads into the mid-gut by means of a constricted valvular opening (oes.vl.).

The mid-gut (m.g.), which is the longest portion of the alimentary canal of this larva, is strongly muscular. Broadest in front, it gradually narrows behind to meet the hind-gut (h.g.).

The hind-gut (h.g.), which occupies the hind third of the larva, is formed of two parts: an anterior and a posterior. The anterior (fig. 17) is a round swollen portion lined with an epithelium of flat cells. It is this portion into which open the malpighian tubules (mlp.) by means of two common ducts. The posterior portion of the hind-gut is muscular and tube-like and a little bent before it reaches the anus. The alimentary canal opens to the outside through a four-grooved anal aperture (figs. 17, 9, an.gr.).

Associated with the digestive system are the salivary glands (sl.gl.) and the malpighian tubules (mlp.). The salivary glands are very minute and lie on either side of the oesophagus. They have the shape of elongated sacs (fig. 20) folded upon themselves. The end of each gland is attached to the abundant fatty tissue by means of small threads. The epithelium of these glands shows large nuclei (n.) with beaded chromosomes (bd.chr.). The ducts from each gland join to form a common duct (sl.d.), which, passing ventrally to the pharynx, opens between the endolabium and exolabium. The common duct shows distinct striae and may therefore be mistaken for a tracheal tube.

The malpighian tubules are four in number, and they enter the front portion of the hind-gut by means of two common ducts. The tubules are very long and convoluted and intimately bound up with the diffuse fat body. Consequently it is often very difficult to dissect them out entire. Each tubule (fig. 21) consists of large cells (cl.), arranged in such a way that the tubule presents a necklace-like appearance. The contents of the tubules show the presence of a number of small deeply staining spherical bodies surrounding the malpighian cells.

Nervous system.—The nervous system consists of a brain made up of the supra-oesophageal ganglia (fig. 22, sp.oes.g.), a sub-oesophageal ganglion (s.oes.g.) and a cord with three thoracic (th.g.) and eight abdominal ganglia (abd.g.). The two-lobed brain lies in the hind region of the head-capsule; the sub-oesophageal ganglion, which lies below the brain, is connected with the latter by right and left commissures forming a ring through which the oesophagus passes behind. The thoracic ganglia (th.g.) are comparatively larger and are situated at short distances from each other. The abdominal ganglia (abd.g.) are somewhat smaller; the ganglia of the various segments are rather wide apart from each other, save the last two which lie close together.

Dissection reveals the heart as a very thin transparent tube lying immediately below the dorsal integument.

Respiratory System.—The respiratory system of the larva of *T. maculipennis*, unlike other Tipulid larvae, consists of two pairs of spiracles. The front pair is carried on the prothoracic segment (fig. 23*c*), and the hind pair is borne on the terminal one. The front spiracles are not found in the newly-hatched larva, but they are quite well-developed in full-grown larvae.

The hind spiracles (fig. 23*a*) are oval in shape, measuring each ·123 mm. in longer axis and ·086 mm. in shorter axis. Each spiracle consists of a central oval plug—" the stigmatic plug " (st.pg.)—formed of deep brown chitin. The chitinous plug has a narrow wavy vertical slit (st.sl.) passing through it and reaching the stigmatic chamber (fig. 23*b*, st.ch.) within. Surrounding the stigmatic plug and separated from it on all sides by quite a broad space is a chitinous rim, called the " stigmatic rim " (st.rm.) of the spiracle. From the sides of this rim radiate a series of chitinous bars (st.br.). Many of these bars are long enough to reach the central stigmatic plug. The stigmatic chamber (st.ch.) thus keeps communication to the outside in two ways : (i) through the narrow wavy vertical slit in the centre of the stigmatic plug, and (ii) through the space between the plug and the spiracular rim occupied by the radially arranged bars.

Keilin (5) asserts that the stigmatic plug-slit is an " artifact " and that the communication between the stigmatic chamber and the outer world is through a perforated membrane that surrounds the plug. Wardle (12), whilst agreeing with Keilin that the slit is brought about by the violent treatment inseparable from section-cutting technique, is of opinion that " it represents a line of incomplete fusion between two portions of the plug which were formerly separate." Moreover, Wardle does not find the presence of any sieve-plate structure in the surrounding chitinised membrane mentioned by Keilin.

Leaving out of account the results of microtome sections, which in the case of the larva of *T. maculipennis* show the presence of a vertical slit, careful dissections of the spiracles of the same larva show that there is a definite narrow wavy vertical slit passing through the stigmatic plug and communicating with the inner stigmatic chamber situated at the base of the plug.

The front and hind spiracles are connected to each other by means of two fairly large tracheal trunks running along the dorso-lateral margins of the body. Various branches are given off from these trunks, which sub-branch and form a network throughout the body.

Pupa.—The pupa of *T. maculipennis* is about 8 mm. long. It is yellow brown in colour, and the body is curved a little in the abdominal region. The breathing horns are well seen on the dorsal side in the prothoracic region. The legs, wrapped in sheaths, are glued down to the body on the ventral side, and so are the wing-pads at the sides. The male pupa is a little smaller than that of the female, and the terminal portions of both show distinctive sexual characteristics as seen in figures 24 and 25. The body of the pupa has a number of small spiny projections (spn.) which are directed backwards. These help the pupa to make its way upwards to the surface of the soil before the adult issues from the pupal skin.

Adult.—The adult *T. maculipennis* is quite a large fly, the female measuring about 8·5 mm. in length and 20 mm. in expanse of wing. The male is a little smaller, being about 7 mm. in length and 19 mm. in breadth with expanded wings. The general specific characters which distinguish *maculipennis* from other species of *Trichocera* are, according to Pierre (10), the following :—

(i) Abdomen uniformly darkish.
(ii) Anterior cross-vein with a distinct patch round it.
(iii) A distinct cloud on and below the base of the radial sector.

The first of these characteristics separates *T. maculipennis* from *T. annulata*; the second, from the rest of *Trichocera* species except *T. regelationis*; while the third distinguishes it from *T. regelationis* itself.

SUMMARY.

(i) The larva of *Trichocera maculipennis* was found in the Cragganmore Distillery refuse at Ballindalloch. It feeds upon the slimy, dark-coloured, odorous residue in the distillery filters, and thus, in habits, plays the part of a scavenger.

(ii) The larvae are found at work in the dirty waste refuse from March onwards till the end of September.

(iii) The adult fly begins to appear in early April, and can be found in large numbers in and near the filter-houses till the end of September. From October till March adult flies have not been observed in the locality.

(iv) A continued examination of the distillery refuse during the autumn and winter months did not indicate the presence of *T. maculipennis* at any stage in the refuse.

(v) The life-cycle of *T. maculipennis*, from the time the egg is laid to the time the adult fly emerges, requires about 40 days under laboratory conditions. The egg-stage lasts from 5 to 6 days; the larva requires about 25 days to complete its growth; the pupal stage extends over a week or so.

(vi) The latter part of the paper deals with the general morphology of the egg, the larva, the pupa and the adult of *T. maculipennis*. A more detailed account of the anatomy of the fully-developed larva is also described.

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ABBREVIATIONS USED.

a. p. = anterior portion.
abd. g. = abdominal ganglia.
abd. m. = abductor muscles.
add. m. = adductor muscles.
an. gr. = anal aperture.
an. pl. = anal plate.
ant. = antenna.
bd. chr. = beaded chromatin.
br. bl. = branched bristles.
br. hn. = breathing horns.
bs. j. = basal joint.
cht. b. = chitinous bands.
cl. = cell.
cly. = clypeus.
cmb. = comblike structure.
cn. d. = concave depression.
d. p. = distal portion.
dr. cd. = dorsal condyle.
dt. st. = dentate structure.
e. = eye.
eg. m. = egg mass.
eg. s. = egg-shell.
end. = endolabium.
ep. = epipharynx.
exo. = exolabium.
f. g. = fore-gut.
f. l. = fleshy lobes.
f. l. a. = anterior fleshy lobe.
f. l. p. = posterior fleshy lobe.
f. ts. = fatty tissue.
hd. = head.
h. g. = hind-gut.
h. sp. = hind spiracles.
j. = joint.
lb. = labium.
lbr. = labrum.
md. = mandibles.
m. g. = mid-gut.
mlp. = malpighian tubules.
mx. = maxilla.
mx. p. = maxillary palp.
n. = nucleus.
oes. = oesophagus.
oes. op. = oesophageal opening.
oes. vl. = oesophageal valve.
pal. = papillae.
ph. = pharnyx.
pr. = projection or process.
p. p. = proximal portion.
p. sp. = prothoracic spiracles.
ps. p. = posterior portion.
r. h. = row of hairs.
sh. l. = shield-like lining.
sl. d. = salivary duct.
sl. gl. = salivary gland.
sns. a. = sensory area.
sns. p. = sensory pit.
s. oes. g. = sub-oesophageal ganglion.
sp. = spiracles.
spn. = spines.
sp. oes. g. = supra-oesophageal ganglion.
st. br. = stigmatic bars.
st. ch. = stigmatic chamber.
st. pg. = stigmatic plug.
st. rm. = stigmatic rim.
st. sl. = stigmatic slit.
t. = teeth.
t. j. = terminal joint.
th. g. = thoracic ganglia.
U. pr. = U-shaped projection.
v. nt. = vertical notch.
wg. pd. = wingpads.

EXPLANATION OF PLATES I–IV.

PLATE I.

FIG. 1. Newly laid egg of *Trichocera maculipennis*, × 75.
2. Egg of *T. maculipennis* after 20 hours, × 75.
3. ,, ,, after 2 days, × 75.
4. Newly hatched larva of *T. maculipennis*, × 75.
5. Fully developed larva, × 7.
6. Thoracic under-surface of the larva, showing the clear spots, each carrying four bristles, × 36.
7. Spiracular region of the larva showing the hind spiracles and the spiracular lobes, × 75.
8. Anal area of the larva, × 75.

PLATE II.

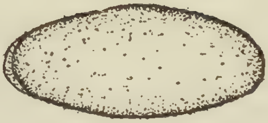
FIG. 9. Anal plate, with anal openings, × 75.
10. Head-capsule of the larva, dorsal view, × 75.
11. ,, ,, ,, ventral view, × 75.
12. Epipharynx of the larva, × 300.
13. Mandible, dorsal view, × 300.
14. ,, ventral view, × 300.

PLATE III.

FIG. 15. Maxillae, labium, × 150.
16. Antenna, eye, × 300.
18. Pharynx (inner view), × 150.
19. ,, (side-view), × 150.
20. Salivary gland, × 75.
20*a*. Nucleus highly magnified, × 300.
21. A portion of malpighian tubule, × 300.

PLATE IV.

FIG. 17. Alimentary canal of the larva, × 17.
22. Nervous system of the larva, × 17.
23*a*. Hind spiracle of the larva, × 400.
23*b*. Vertical section of the hind spiracle, × 400.
23*c*. Front spiracle, × 300.
24. Female genitalia of the pupa, × 75.
25. Male genitalia of the pupa, × 75.



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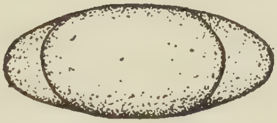

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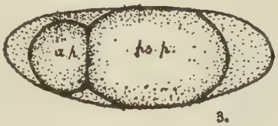

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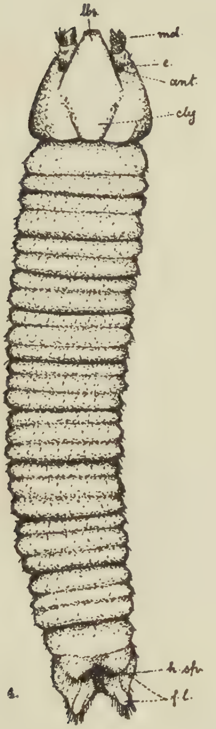
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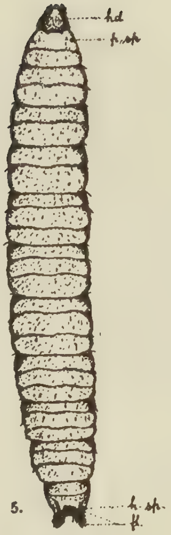
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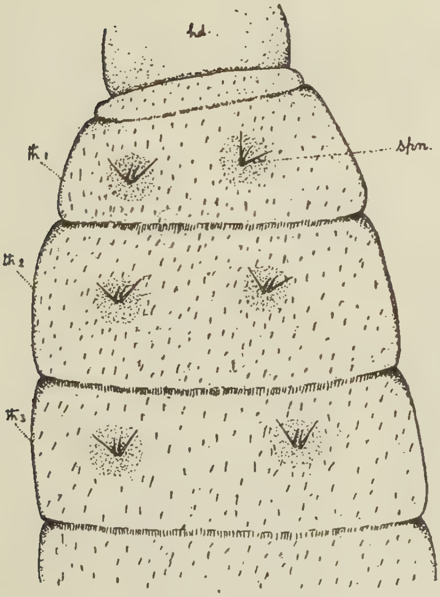
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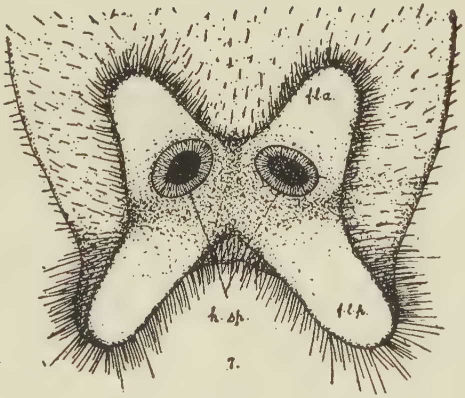

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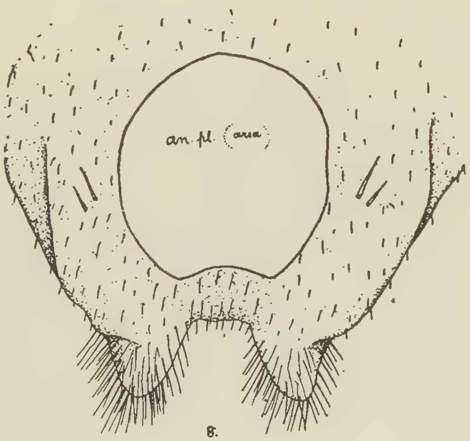

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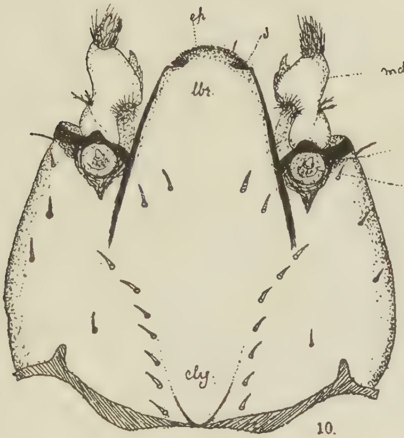
Structure and Bionomics of *Trichocera maculipennis*, Mg.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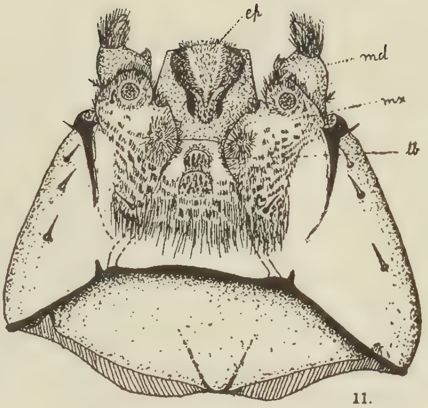

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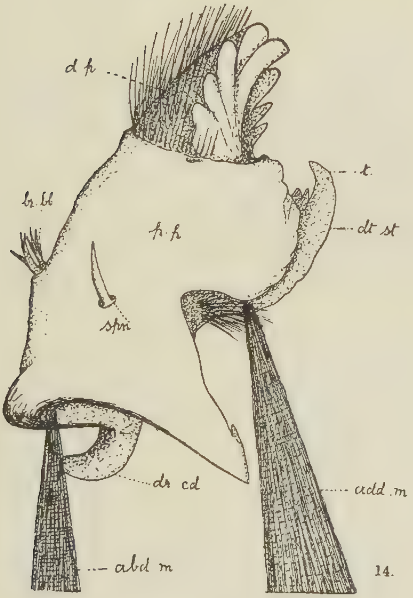
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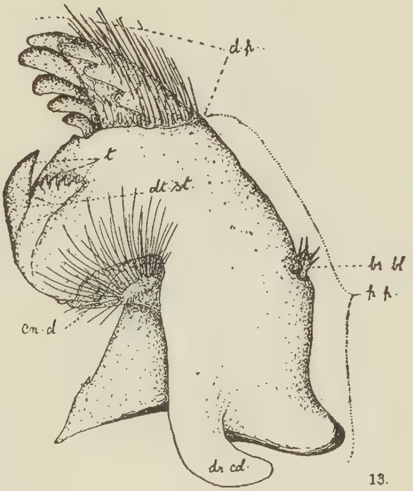
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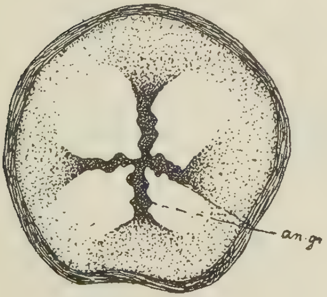

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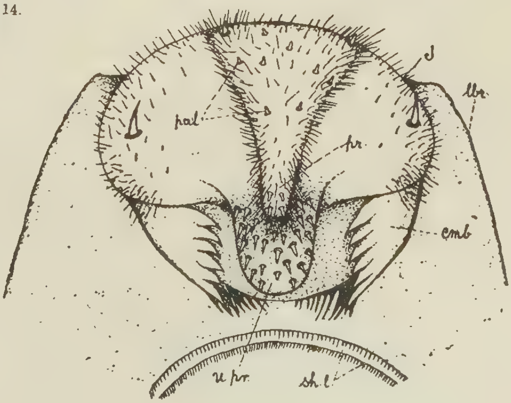
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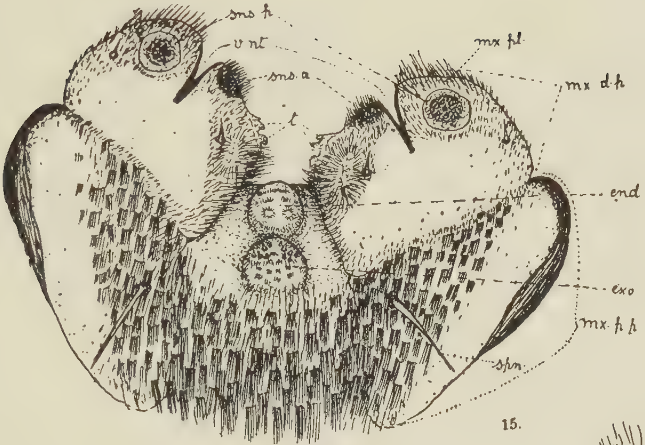
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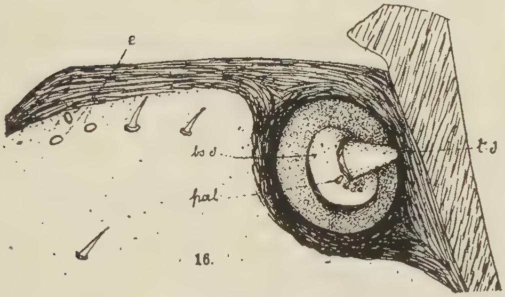

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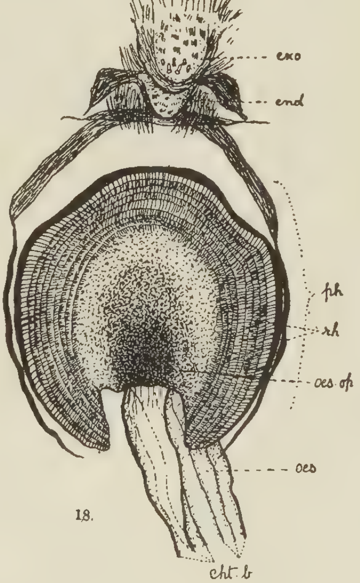
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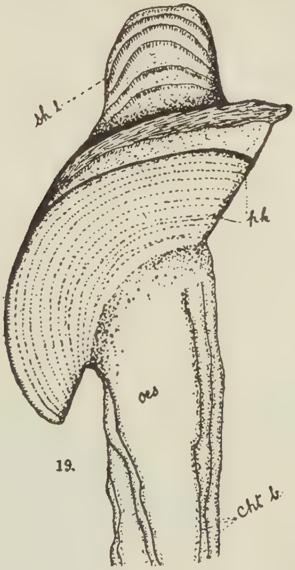
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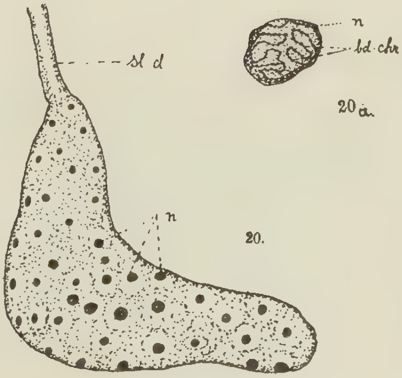
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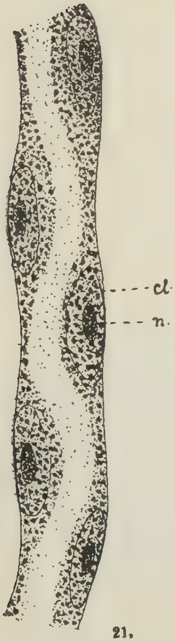

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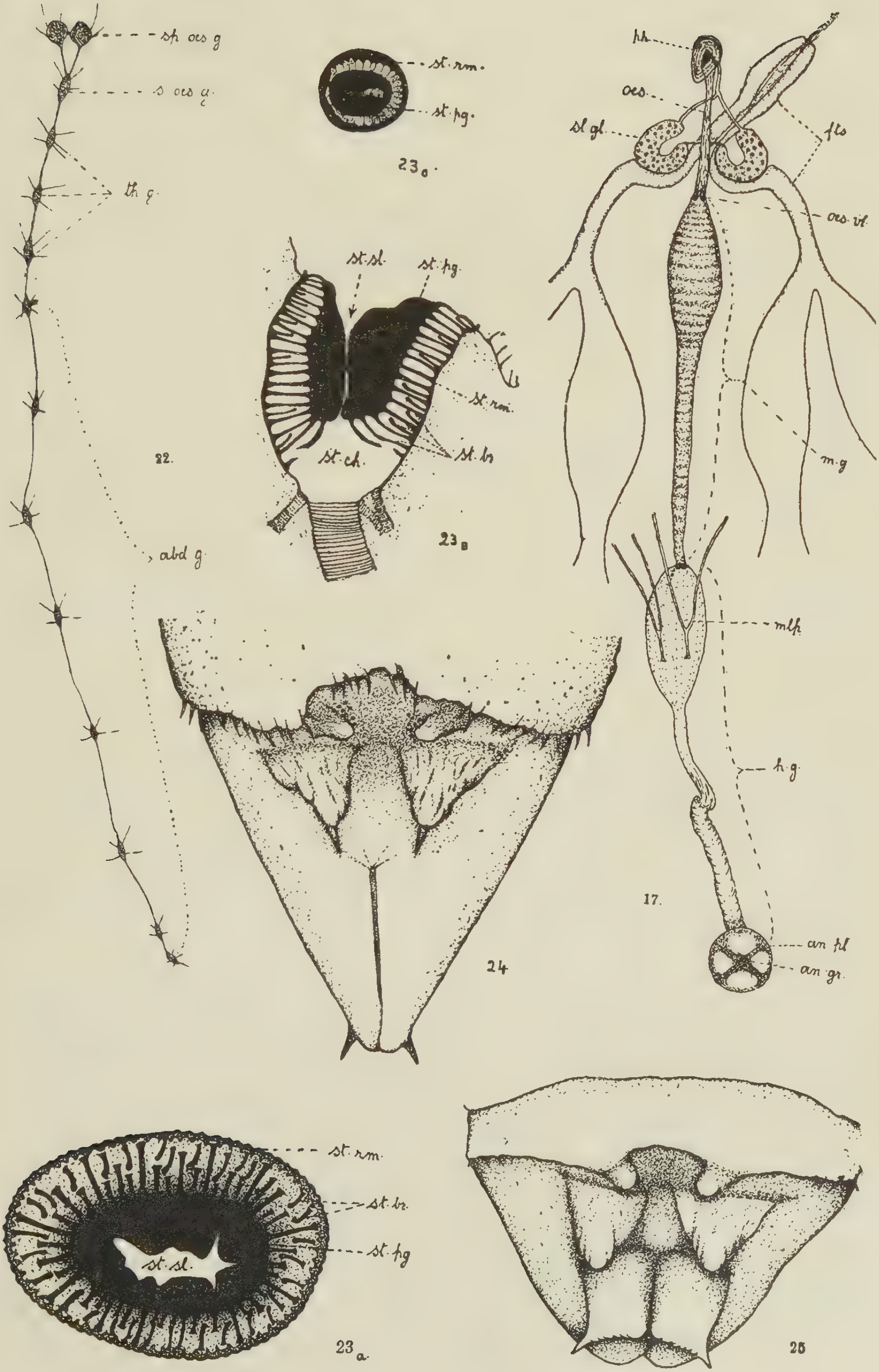
Structure and Bionomics of *Trichocera maculipennis*, Mg.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Structure and Bionomics of *Trichocera maculipennis*, Mg.

ON THE METAMORPHOSIS OF THE ALIMENTARY CANAL IN CERTAIN EPHEMEROPTERA

By Alan Pickles, B.Sc.

(Entomologist to the Trinidad Froghopper Investigation Committee).

[Read 5th November, 1930.]

With Plates V and VI.

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1. Introduction.

Although the Ephemeroptera as a whole have attracted popular and scientific attention to a considerable extent from time to time, the literature dealing with the special study of the alimentary canal is relatively scanty. This is the more surprising since it is in the alimentary canal that the most profound changes have long been known to occur in these insects: changes which are perhaps unparalleled in any other Order.

The period of time occupied by a single life-history is not known accurately, but nymphal life probably extends over three or four years. The nymphal instars are succeeded by a winged subimaginal stage of brief duration—usually only a few hours—and this in turn by the imaginal stage, the existence of a subimago being characteristic of the Ephemeropteran life-history.

Both subimago and imago are capable of active flight, but the former is usually more or less quiescent unless disturbed.

Imaginal life is relatively brief, sufficient only to allow of pairing and oviposition. In some cases, the imago emerges and dies on the same day, hence the name ἐφήμερον applied to these insects by Aristotle.

In the nymph, the alimentary canal presents no very unusual features, but in the imago it is no longer capable of maintaining digestive functions. The muscular coat of the mesenteron disappears to a great extent, and this part of the digestive tract becomes excessively thin-walled and is frequently distended with gas. In consequence of this distention, the change in structure has often been regarded as an adaptation to aerial existence whereby the insect, in deflating or inflating the mesenteron, is able to alter the specific gravity of its body at will. To the possession of such an adaptation is attributed the peculiar dancing flight of these insects. The alteration in the alimentary canal is accompanied by atrophy of the mouth-parts (12).

In his great posthumous work (13), Swammerdam suggests the possibility of such a change: "Noch een andere reeden isser waar door het Haft luchtig op het water vliegt, dewelke bestaat in dat se een subtiel blaasken met lucht binnen in haar lichaam hebben: ten sij men sou willen seggen, dat haar Maag op die tijt met Lucht vervult was. . . ." This account is accompanied by illustrations setting forth the general morphology of the nymphal gut and constitutes a valuable contribution to the subject.

Vayssière (15) gives an account of the nymphal structure in numerous Ephemeroptera and devotes a separate chapter of his paper to the digestive system in these insects. The greater part of this chapter, however, is given up to a consideration of mouth-parts. He points out that of the mesenteron, the anterior part is chiefly glandular, while the posterior part is characterised by its well-developed musculature. The whole of the alimentary canal posterior to the openings of the Malpighian tubes, Vayssière calls "rectum," in which he describes "un fort bourrelet interne . . . qui s'étend d'une extrémité a l'autre de cette région intestinale."

Palmèn (8) devotes a section of his treatise (pp. 45, 53 *et seq.*) to the development of the alimentary canal of Mayflies. He states that the mesenteron becomes widened and thin-walled in the imago, suggesting that air is taken into the alimentary canal by the subimago and that the pressure of this air is responsible for the changes in morphology. This author further describes the atrophy of the muscular coat of the mesenteron, stating that during the process of dissolution, the muscles have an appearance as if they were undergoing fatty degeneration. The function of the imaginal gut is considered to be connected primarily with the ejection of the genital products, and the probability of an aerostatic function in addition is admitted.

Fritze (5) describes the structure of the whole alimentary canal in considerable detail, dealing separately with conditions found respectively in the "larva," "nymph," subimago and imago of several species. A special point is made of the structure of a valve in the proctodaeum of the imago, which is interpreted as a modified part of the ileum. The dilation of the mesenteron and the flattening of its epithelium is regarded as due to the intake of *water* by the nymph, shortly before the emergence of the subimago, which water is later replaced by air.

Subsequent workers, Leue (6), Drenkelfort (2) and Sternfeld (12), would appear to accept this explanation of the morphological changes.

Leue considers certain thickened regions of epithelium, which he somewhat unfortunately calls "Imaginalringe," to be regions of growth, wherefrom new cells are constantly added to the epithelium of that portion of the gut immediately posterior to them, throughout nymphal life.

Drenkelfort expresses a doubt as to the possibility of such inflation of the gut that the specific gravity of the insect is diminished appreciably.

Sternfeld describes the development of the stomodaeal musculature, and shows that in the imago the stomodaeum might function as a powerful pump for forcing air into the mesenteron.

2. MATERIAL AND METHODS.

The material examined in the course of the present investigations consists of :—

Ephemerella ignita, Poda,
  Nymphs, subimagines, imagines.
Leptophlebia meyeri, Eaton,
  Nymphs, subimagines, imagines.
Ephemera danica, Müller,
  Nymphs, subimagines, imagines.
Chloeon sp.,
  Nymphs.
Baëtis spp.,
  Nymphs.
Baëtis binoculatus, Linn.,
  Subimagines.
B. pumilus, Burm.,
  Imagines.
B. rhodani, Pictet,
  Imagines.

Eaton's monograph (4) and his Concise Synopsis (3) were consulted for the identification of winged insects; nymphs were identified from Rousseau's descriptions (11).

Imagines of *Baëtis pumilus* and *B. rhodani* were taken as such in the field; all other winged insects were obtained by breeding in captivity.

The fluid of Carnoy-Lebrun was the most generally used fixative and gave good results with all stages, especially when the material was incised before fixation. Bouin's Picro-formol and Carl's formula were quite useless.

Material was embedded in paraffin or in celloidin and paraffin; sections were stained on the slide with Haidenhain's Iron Haematoxylin or Mayer's Haemalum.

Most of the work was carried out with *Ephemerella ignita* and *Ephemera danica.*

3. Structure and Metamorphosis of the Alimentary Canal.

(i) *The Nymph, prior to Metamorphosis.*

General Form.—The alimentary canal of the nymph falls into three well-defined regions: stomodaeum, mesenteron and proctodaeum. Of these, the stomodaeum is confined to the head, extending from the ventrally placed mouth to the anterior margin of the prothorax. The mesenteron, which is much the longest division, runs from its junction with the stomodaeum to about the middle of the seventh abdominal segment, where it joins the proctodaeum. The proctodaeum opens to the exterior by the anus in segment ten. From the region of junction of the mesenteron and proctodaeum in segment seven, numerous Malpighian tubes originate and lie in the haemocoele in a somewhat irregular fashion. Apart from the Malpighian tubes, there are no diverticula of the alimentary canal, caeca and salivary glands alike being absent.

The alimentary canal attains its greatest diameter in the mesothorax; before and behind this region, the mesenteron narrows gradually until at the posterior end the diameter is about one-tenth and at the anterior end one-third of this maximum.

The stomodaeum is a much narrower tube and projects some little distance into the anterior end of the mesenteron, forming with the anterior part of the mesenteron a simple oesophageal valve (Pl. V, figs. 1, 5).

The procotodaeum is clearly subdivided into three regions, which are respectively, from before backwards, the ileum, colon and rectum.

In the nymph, the alimentary canal is not convoluted, but nymphs of *Ephemera danica* differed from all the others examined in having the mesenteron transversely ridged internally, especially in the thoracic part of its course.

The Stomodaeum.—The stomodaeum is lined internally by a distinct and well-developed chitinous layer. The epithelial layer beneath this is thrown into large longitudinal folds, so that in transverse section the lumen of this region has a distinctly stellate appearance (Pl. V, fig. 3). The cells of the stomodaeal epithelium are short and columnar, with oval nuclei (Pl. V, fig. 4).

Surrounding the epithelium is a layer of circular muscles; the posterior half has also a sheath of longitudinal muscles. In addition, radial muscle bundles are present, connecting the stomodaeum with the exoskeleton of the head.

Before its entry into the mesenteron, the stomodaeum dilates slightly; this dilation is well marked in *Ephemera danica.*

The stomodaeum projects slightly into the mesenteron (about 0·05 mm. in fully-grown nymphs in *Ephemerella ignita* on the ventral side) to form an oesophageal valve, in which the epithelium of the stomodaeum joins on to that of the mesenteron without a break. The circular muscle layer continues into the fold of the oesophageal valve (Pl. V, fig. 5, c.m.) and is continuous with the circular muscle sheath of the mesenteron; the longitudinal muscles, on the contrary, end on the anterior part of the mesenteron and do not enter into the fold of the valve (Pl. V, fig. 5, l.m.). Dorsally, the oesophageal valve does not extend so far backward as it does ventrally.

Where the stomodaeal epithelium abuts on that of the mesenteron, it is raised into a ridge of *Ephemerella ignita* and *Baëtis* spp. Cell walls cannot be distinguished in this region, and the nuclei are small and crowded. Leue (6) regards this as a region of mesenteric growth, from which new cells are cut off and added to the mesenteron, thus accounting for growth in length of that division of the alimentary canal. He records having observed nuclear division in this part, which he calls an " Imaginalring." It has not been possible to verify this observation in the present investigations.

The Mesenteron.—The layers of the wall of the mesenteron are: on the outside, an exceedingly delicate peritoneum, which can only be discerned with difficulty, enclosing the muscular sheaths which in turn enclose the epithelium. The outer muscular layer consists of longitudinal fibres and is best developed in *Ephemera danica*; in *Ephemerella ignita*, it is absent except at the anterior and posterior ends of the mesenteron. The inner muscle layer consists of circular muscles.

The layer of epithelium consists of columnar cells having the form of fairly regular hexagonal prisms. The anterior epithelial cells, including those reflected to establish connection with the stomodaeum are crowded, especially at their inner ends, with dense, black inclusions (Pl. V, fig. 5). These inclusions are extremely dense and conspicuous, even in unstained sections. A thick and brilliant " striated hem " (Miall & Denny, 7) covers the free ends of the cells in the anterior part of the mesenteron, giving the epithelium a ciliated appearance at first sight. This striated hem disappears in the part posterior to the fifth abdominal segment. In *Ephemera danica* the striated hem is present, but is not very conspicuous (Pl. V, fig. 6). Some of the epithelial cells, especially the more anterior ones, have their free surfaces produced into rounded vesicles which encroach upon or even protrude through the striated hem; they probably represent a phase in the secretion of digestive ferments. Such vesicles do not appear to be produced in the region where no striated hem is visible.

A peritrophic membrane could not be distinguished in sections, but it was observed that the faeces of fully developed nymphs of *Ephemera danica*, voided prior to ecdysis, were enclosed in delicate, transparent sacs.

Food material observed in the mesenteron consisted largely of filamentous algae and diatoms; the latter were often so abundant as to injure the knife seriously during section cutting.

The muscular layer of the mesenteron is most strongly developed at the posterior end of the mesenteron, where it attains the same thickness as the epithelial layer, which is here somewhat reduced.

The Proctodaeum.—The proctodaeum exhibits three well-marked divisions. Of these, the ileum has the form of a short truncated cone, with the base anterior and giving off numerous Malpighian tubes as radial diverticula. The wall of the ileum, as of the rest of the proctodaeum, consists of the layers: peritoneum, circular muscles and epithelium, and has a chitinous lining. In section, the epithelium has a remarkably fibrillar appearance (Pl. V, fig. 7). At the free border of the epithelium, the striations are finer and more regular than elsewhere, giving this portion a certain resemblance to the striated hem of the mesenteron. This border is somewhat sinuous, so that the depth of the epithelium is greater in some places than in others. The nuclei are large and granular; towards the anterior and posterior limits of the ileum they decrease a little in size. Radial cell-walls are not evident and are probably entirely absent, at least in *Ephemerella ignita.*

In the colon, two kinds of epithelium may be distinguished, one containing large nuclei (Fritze, *loc. cit.* "*grosskerniges Epithel*") and one much more delicate, with small nuclei (*ibid.* "*kleinkerniges Epithel*"). The arrangement of these epithelia varies with the species. In *Ephemerella*, *Baëtis* and *Leptophlebia*, a transverse section (Pl. V, fig. 8) shows that there are three bands of "*kleinkerniges Epithel*" alternating with three of "*grosskerniges Epithel*," with the latter dorsal and ventro-lateral in position. The ventro-median edges of these large bands frequently project into the lumen of the colon; it seems possible that it may be such a projection and not a definite structure which Vayssière describes as ". . . . un fort bourrelet interne" (cf. Vayssière 15, fig. 38). In *Ephemera danica* there are only two bands of each type; those of "*kleinkerniges Epithel*" are dorsal and ventral in position. According to Fritze and to Drenkelfort, *Ecdyurus fluminum* (Lin.) and *Siphlurus lacustris*, Eaton, have only one band of each kind. In general appearance the "*grosskerniges Epithel*" closely resembles the epithelium of the ileum; it is fibrillar, with large, granular nuclei, and, except in *Ephemera danica*, with no suggestion of radial walls (Pl. V, figs. 8, 9 and 10). Each of its bands is pressed closely against the muscular sheath, except at the edges, where it tends to become free and to project into the cavity of the gut as described above. The bands of "*kleinkerniges Epithel*" are continuous with these; each is very narrow and rather irregular, containing small nuclei which enclose two or three chromatic bodies (Pl. V, fig. 9).

Towards the posterior end of the colon the "*kleinkerniges Epithel*" enters more and more into the composition of the gut-wall by encroaching on the "*grosskerniges Epithel*" and finally replacing it altogether. In this way, the colon merges into the rectum, in which the epithelium is all of the small nucleate type (Pl. VI, fig. 11).

The depth of the rectal epithelium varies to some extent, but is, in the main, greater than that of the "*kleinkerniges Epithel*" in the colon. Surrounding it is a layer of circular muscles, which, in transverse section, show very fine histological details. Radial muscles also are present, and, just anterior to the anus, the circular muscles are greatly developed to form a sphincter. In the first half of its course in *Ephemerella ignita* the wall of the rectum is depressed all around in such a way that the lumen is almost obliterated for a little distance and a rectal valve (Pl. VI, fig. 11, rect. v.) is thus formed. The muscular coat as well as the epithelium is involuted to form this structure.

Outside the anus, the rectal epithelium is continuous with the hypodermis.

(ii) *The late Nymph and the commencement of Metamorphosis.*

The approach of the ecdysis which is to liberate the subimago is evidenced by a very marked darkening of the colour of the nymph in all the species examined. This darkening begins on the dorsal side of the thorax and extends slowly in all directions until, at the end of two or three days, the nymph has assumed a very dark grey coloration over its whole surface. Such nymphs become sluggish in habit, even the respiratory movements of the gills being a little slowed down. In most cases, the gut is emptied of food during this time, though exceptionally, the whole process may take place with food remaining in the alimentary canal.

When darkening of the cuticle is completed, bubbles of gas may be noted beneath the nymphal cuticle, especially in the thoracic region; the wing rudiments in particular are filled and often distended with gas. In consequence of the increased buoyancy imparted thereby, the nymph rises from the substratum and floats passively at the surface of the water. Should the nymph be disturbed in this condition it makes violent and aimless swimming movements, recalling those of the pupae of many of the higher aquatic insects. After a time the nymphal cuticle splits longitudinally in the thoracic region and the subimago rapidly makes its way out.

The subimago of *Ephemera danica* emerges about three hours after the nymph has commenced to float; males on an average emerge more quickly than females, and the male subimago and nymph tend to be rather smaller than those of the female.

Considerable internal changes take place at this time. The diameter of the mesenteron is considerably reduced, apparently as a direct consequence of the absence of gut contents: if the alimentary canal of a living nymph be dissected out, small portions of it can be emptied of food by gentle washing, when it is found that such portions contract to a very small size.

A striking appearance observed in nymphs of *Baëtis* spp. and of *Leptophlebia meyeri* at this stage is that blood corpuscles are aggregated in dense swarms along the course of the mesenteron and proctodaeum.

As a result of the contraction, the epithelial cells of the mesenteron become somewhat distorted; the cells also lose their well-defined boundaries, the radial walls ceasing to be visible and the free surfaces becoming very irregular. At the same time the protoplasm near the free surface becomes very coarsely granular (Pl. VI, fig. 13).

This condition is followed by a very striking one in which cell material is extruded in the form of vesicles into the lumen of the alimentary canal. Each of these vesicles is a spherical body containing a clear, refractive substance, and a few bodies which take up nuclear stains very readily (Pl. VI, fig. 14). Indeed, many of the vesicles are very similar to nuclei in appearance and size at this time. The true nuclei of the epithelium have meanwhile become reduced in size and contain a few chromatic granules. It has not been possible to correlate these changes with any nuclear division or reduction process. In consequence of this loss of cell material the epithelium becomes reduced to a much thinner, somewhat irregular layer, containing degenerate nuclei.

The process of epithelium reduction described above appears to be the typical one and was observed in every case examined. In *Ephemerella ignita* and *Leptophlebia meyeri*, however, the process occurs in a modified form in most parts of the mesenteron, though the typical process does occur in some parts, particularly at the posterior end. In these cases the cell boundaries are not lost in the early stages, but the contents of the cells appear to separate into two fractions—one optically denser and more granular, which collects at the base of the cells, and a clear fraction which fills that half of the cell nearer the gut lumen (Pl. VI, fig. 15). The epithelium thus comes to present the appearance of a squamous epithelium with granular contents, supporting a series of delicate arches which are the cell-walls enclosing the clear material.

This is apparently a specialisation of the more typical process, in which the whole of the inner part of the epithelium cell is converted into one vesicle of rejected cell material.

In *Ephemera danica* the muscular coats of the mesenteron also undergo a change while these alterations are proceeding in the epithelium. The bundles of muscle fibres, which are distinct in younger nymphs, now become ill-defined, the peritoneum breaks down in places and blood cells enter through the openings so formed (Pl. VI, fig. 13). The other species examined also show the beginnings of a similar change in the muscular coat, but pronounced muscular degeneration is more characteristic of the next instar.

The stomodaeum does not undergo so marked a change; only in the neighbourhood of the oesophageal valve is any alteration observed. Here, the stomodaeal epithelium entering into the formation of the valve becomes apparently reduced in amount, and in all the material, except *E. danica*, the valve itself tends to become directed transversely across the lumen instead of backwards as in earlier stages. It has not been possible to obtain preparations showing histological change in this tissue. Congregation of blood corpuscles does not take place to any great extent around the stomodaeum except in the neighbourhood of the oesophageal valve.

In metamorphosing nymphs of *Baëtis* sp., blood corpuscles were observed to cluster quite as abundantly around the proctodaeum as they did around the mesenteron; there was, however, no reason to believe that they penetrated into the muscles and no histological change was observed in this region.

It is of interest to note that the blood corpuscles of the late nymph consist almost exclusively of small cells, oval or circular in optical section, 5–8 μ in diameter; younger nymphs have a considerable proportion of large fusiform corpuscles exceeding 12 μ in length (measurements obtained from *E. danica*). This alteration in the constitution of the blood is worthy of further study.

(iii) *The Subimago.*

The processes of metamorphosis of the alimentary canal in the subimago are a direct and probably unbroken continuation of those recorded above in the full-grown nymph. In some individuals the alimentary canal was contracted even to a greater extent than in the late nymph, so that the dorsal and ventral walls of the mesenteron were actually contiguous in parts (Pl. VI, fig. 16). This extreme contraction characterises newly emerged subimagines.

The state of degeneration of the mesenteron at the time of the emergence of the subimago varies considerably, but appears to be more or less constant for a given species. In general, the newly emerged subimago of *Ephemera danica* seems to be most advanced in this respect and that of *Ephemerella ignita* least so.

Apart from local changes in general form, associated with the reduction of mouth-parts, the stomodaeum remains practically unchanged. Histological change does occur, however, in the stomodaeal portion of the oesophageal valve, slightly anterior to its apex. Here for a little distance in *Ephemerella ignita* the epithelium shows distinct signs of degeneration : the radial cell walls are lost, the protoplasm becomes coarsely granular, and the tissue generally becomes indefinite in structure.

In the mesenteron a wide range of conditions may be found in this instar, even in different parts of one individual. The protoplasm of the epithelium condenses still more towards the bases of the cells, and there is a certain amount of extrusion of clear material in the form of vesicles into the lumen of the gut. In *Ephemerella ignita* large terminal vacuoles are still present in most of the epithelium cells when the subimago is newly emerged (Pl. VI, fig. 16). As these processes continue, the cytoplasm still remaining becomes very coarsely granular with the granules aggregated into clusters (Pl. VI, fig. 17); the nuclei become very indistinct by loss of their contents and ultimately disappear for the greater part. The vacuoles also become detached or ruptured, leaving behind an extremely thin and almost structureless layer to represent the epithelium. As this condition is attained in the several parts of the mesenteron, inflation of that part seems to occur, so that the completely metamorphosed mesenteron is distended along its whole length. The portion of the mesenteron lying in the prothorax retains its nuclei and its cellular nature generally, but a striated hem is absent and the cytoplasm is free from granules.

While these changes take place in the epithelium, dissolution of most of the muscular coat of the mesenteron proceeds apace. The process is essentially similar to that described as occurring in the late nymph of *Ephemera danica* : the individual muscles lose their definition, the layer becomes coarsely granular in parts and invasion by blood corpuscles occurs. Certain blood corpuscles become swollen and contain dark, granular inclusions. The muscular coat becomes thinner and thinner, ceases to be sharply marked off from the degenerating epithelium and ultimately disappears, except at the anterior and posterior ends of the mesenteron.

In *Ephemera danica* the epithelium of the ileum and colon was observed to be reduced in thickness at this stage, though normal nuclei were retained. The development of this condition, which is not found in the other species, was not traced.

Distention of the reduced mesenteron causes displacement of certain parts of the alimentary canal, but apparently without any fundamental morphological change in those parts. The ileum is particularly involved : in *Ephemerella ignita* it becomes completely telescoped into the colon, or displaced to one side of it, so that ileum and colon both lie in the same segment. In *Ephemera danica* the anterior part of the ileum is diverted to lie across the lumen of the alimentary canal, and forms, with the hinder part of the mesenteron, a valve between the mesenteron and the proctodaeum.

Eclosion of the imago occurs about the time when all the foregoing changes are completed, but the exact state of completion is subject to slight variation.

(iv) *The Imago.*

In some few cases the last stages of mesenteron reduction may occur after the final moult. With this exception the alimentary canal persists for the remainder of the insect's life in the condition described above for the subimago immediately before moulting finally (Pl. VI, fig. 20).

4. Conclusions.

The observations of Palmèn and of Fritze led those investigators, as indicated in the introduction, to regard the change in structure of the mesenteron as the simple and direct result of mere mechanical pressure. The former considers that *air* pressure is responsible for initiating and completing the change, while Fritze contends that *water* pressure is first exerted, just before the subimago emerges: "Nach Ausstossung der festen Nahrung durch die Nymphe unmittelbar vor dem Ausschlüpfen des Subimago tritt das Wasser mit ziemlicher Kraft in den Darm, welcher hierdurch ausgedehnt wird. . . . Diese Ausdehnung halte ich für die einzige Ursache der Verwandlung" (5, p. 17).

It would appear, since no account of actual observations of the process is given by either author, that these views are simply hypotheses to be accepted or rejected on their merits. In effect, Fritze accepts his predecessor's explanation, but suggests another dilating agent—water instead of air—because, on bisecting a subimago under water, no gas escaped from the alimentary canal, while gas did escape when an imago was so treated. On the other hand, Eaton (4, p. 9) states distinctly that gas is present in the alimentary canal when the subimago is about to emerge: "The change from nymph to subimago is effected while the insect is floating at the surface of the water, buoyed up by gas which has accumulated within the alimentary canal and between the new and the old integuments of the body" (*loc. cit.*).

Direct observation of the alimentary canal in living specimens is almost impossible; in the late nymph the accumulation of air between the old and new cuticles renders the body-wall quite opaque, while, in the subimago, the chitin is characteristically dull and impenetrable. Repetition of Fritze's experiment of bisecting the living insect under water confirms his view in the case of the subimago of *Leptophlebia meyeri*, that this time the alimentary canal does not contain gas under pressure, since two minute bubbles alone appear at the cut end of the body, and these only when the body is pinched gently. This experiment has been repeated many times with young subimagines of *Leptophlebia meyeri*, always with precisely the same results.

It has been shown above that in all cases examined, where the gut contents had been expelled before the transformation of the alimentary canal commenced, the lumen was narrower in the late nymph and early subimago than in younger nymphs, and dilation was not observed in the sections until this transformation was nearly completed. The regularity with which this occurred would seem to preclude the possibility of its being due to an artefact, and such a condition is obviously incompatible with a state of high internal pressure. The explanation given by Palmèn and Fritze cannot therefore be accepted.

In following the fate of the muscles in the wall of the mesenteron, Palmèn observed a gradual resolution of the fibres into a homogeneous granular mass "etwa als waren sie fettig degeniert," and he does not suggest that this change is due to the same cause as is the alteration in the epithelium.

Histological research on the higher insects since Palmèn's time has shown that in many cases the blood corpuscles play an important part in the process of metamorphosis, probably by ingesting and removing from their original situations various tissue elements which are no longer required there. It has been shown earlier in the present paper that prior to the emergence of the subimago there is a characteristic crowding of corpuscles around the mesenteron, and there seems to be no doubt that a process of true phagocytosis of the muscular coat of the mesenteron occurs in the Ephemeroptera. This view is supported by the fact that free cells with large inclusions may be seen in the haemocoele, which are regarded as blood corpuscles containing debris from the break-up of muscle. In many places, corpuscles may be distinguished lying among the muscles at this stage, beneath the very delicate peritoneum which they have penetrated. It is interesting to recall in this regard Palmèn's statement that the condition of the muscles resembles fatty degeneration—an appearance which, according to Pérez (9), constantly accompanies phagocytosis.

In a Chrysomelid beetle, Poyarkoff (10) describes a metamorphic process in the hypodermis which resembles in many respects the change here described in the mesenteric epithelium of *Ephemera danica*. According to Poyarkoff, certain cells in the affected tissue elongate and divide mitotically while the larva is still active. A single large granule appears in the nuclei of such cells and is passed into the cytoplasm, thence into the haemocoele or an intercellular space, together with a mass of cytoplasm which surrounds the granule. Poyarkoff regards this as a process of " rejuvenation " whereby a cell " peut passer a un état moins différencié en rejetant une partie de sa substance, et se différencier ensuite dans un autre sens."

The process described for the Ephemeroptera, however, differs from " rejuvenation " as defined by Poyarkoff in the following particulars :—

(1) It has not been possible to correlate the process in Ephemeroptera with a preceding nuclear division.
(2) The vesicles of rejected cell matter contain granular inclusions which are not definitely known to be of nuclear origin.
(3) Eliminated matter is passed into the lumen of the gut and not into the haemocoele or an intercellular space.
(4) Cells which have undergone the process remain reduced.

In spite of these differences, it may be possible to reconcile the phenomena in the Ephemeroptera with true rejuvenation up to a point.

(1) It is doubtful to what extent cell division is an essential part of the process of rejuvenation. Tiegs (14) considers that metamorphic processes such as rejuvenation occur when the volume-surface ratio of cells becomes too great for efficiency in nutrition and respiration; the natural reaction to such a condition in cells forming a tissue would be volume reduction either by throwing out cell material or by cell division, but probably not both in the simplest cases.
(2) Although the granules present in the eliminated vesicles have not been traced to a nuclear origin, it seems probable that nuclear material is voided by the cells since there may be reduction of chromatin material to the point of disappearance of the nuclei.
(3) The mode of disposal of eliminated matter may be explained by a consideration of the situations of the tissues involved in the two cases. It must be admitted, however, that material passed into the haemocoele might become available for a subsequent histogenesis,

while material passed into the lumen of the gut is not likely to become available.

(4) Although in the Ephemeroptera, cells which have parted with the bulk of their substance remain in a reduced condition throughout the rest of the life of the insect, it is probably incorrect to say that re-differentiation does not occur in the mesenteric epithelium. At the beginning of the reduction process there is one type of tissue, and at the end there is another—both adapted to special purposes.

There seems to be at least a prima-facie case for considering tissue reduction in the Ephemeroptera homologous with rejuvenation.

Carpenter (1, pp. 192 and 333) regards the Ephemeropteran subimago as the homologue of the pupa of Holometabola. He suggests that one ecdysis after the development of functional wings was originally the rule, and that the first winged instar is represented in Ephemeroptera by the subimago, in Holometabola by the pupa. In support of this, he adduces the large size of the external wing rudiments in the less specialised pupae, such as those of many Coleoptera and Neuroptera and the relatively great activity of those pupae.

This suggestion is in accordance with the facts observed in the present study, and, together with those facts, prompts the following view of the development of the insectan metamorphosis. In the Ametabola, formation of the imago occurs gradually during nymphal life and the extent of the development becomes apparent externally after each ecdysis. During the course of the evolution of higher insects, this development becomes postponed to the later instars in the case of a greater or lesser number of organs and tissues, either by a progressive holding up of development or, on Tiegs's view, by a loss of the power of division by the nymphal cells. In the latter case, formation of imaginal tissue only begins when the volume-surface ratio is too great for efficiency and cellular death is threatened. Development in either event would tend to be concentrated into the later nymphal instars and even to extend into the subimaginal stage which we are postulating as common to all insect life-histories. Such a condition persists, as we have seen, in the life-history of some Ephemeroptera such as *Ephemera danica.* Still later in phylogeny, more of the tissue transformation became postponed until the subimaginal stage was attained, so that although the processes continued to be initiated in the nymph, they became more and more definitely associated with the subimago. Greater specialisation in the form of both nymph and imago resulted in a more profound metamorphosis occurring in the subimago, which consequently became incapable of active life, and so the quiescent pupal stage was derived. Although the recent Ephemeroptera cannot be regarded as on the direct line of evolution of the Holometabola, the Order exhibits within itself a parallel to part of such a course of development, for, as has been shown, in *Ephemerella ignita* and *Baëtis* spp., more of the transformation is held up until the subimago emerges than in the case of *Ephemera danica.* A study of wing-venation in these types tends to the view that *Ephemera danica* is the most primitive of the three and *Baëtis* the most specialised.

5. Summary.

1. An extensive change in the structure of the mesenteron occurs in the types studied, during which the epithelial and muscular layers become reduced and form in the imago an extremely thin membrane.

2. This change commences in the last nymphal instar shortly before the emergence of the subimago, and is completed in the latter stage or immediately after the imago emerges.

3. The attenuation of these layers is not brought about by simple mechanical pressure, as has been suggested, but is accompanied by phagocytosis and a phenomenon considered to be comparable to " rejuvenation."

4. The mesenteron is the principal region of the alimentary canal affected, but a specialised region of the stomodaeum is involved, and there may be some attenuation of the ileum and colon in addition.

5. Arguments are adduced in support of the view that the subimago is the homologue of the pupa of Holometabola.

6. Acknowledgements.

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EXPLANATION OF PLATES V AND VI.

Abbreviations.

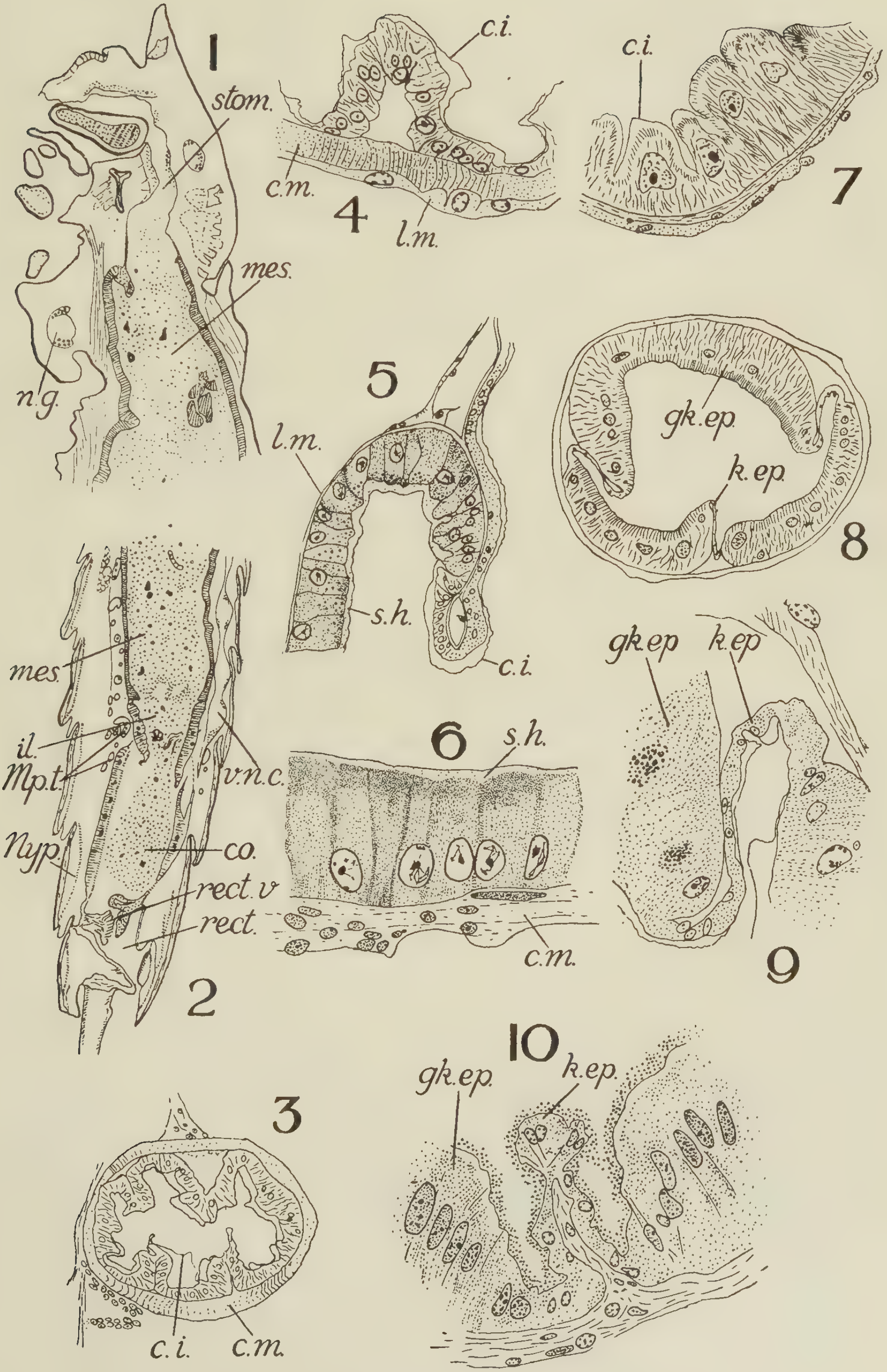
an.	anus.	mes.	mesenteron.
b.c.	blood corpuscles.	n.g.	nerve ganglion.
c.i.	chitinous intima.	od.	oviduct.
c.m.	circular muscle layer.	ov.	ova.
co.	colon.	oes.v.	oesophageal valve.
ep.	epithelium.	p.	peritoneum.
gk. ep.	" grosskerniges epithel."	rect.	rectum.
hyp.	hypodermis.	rect. v.	rectal valve.
il.	ileum.	s.h.	striated hem.
k. ep.	" kleinkerniges epithel."	stom.	stomodaeum.
Mp. t.	Malphigian tubes.	v.n.c.	ventral nerve cord.

PLATE V.

FIG. 1. *Ephemera danica;* nymph; head and thorax, L.S.
2. *Ephemerella ignita;* nymph; abdomen, L.S.
3. *Ephemera danica;* stomodaeum, T.S.
4. *Ephemera danica;* part of stomodaeum, T.S., more highly magnified.
5. *Ephemera danica;* nymph; L.S., through the oesophageal valve.
6. *Ephemera danica;* nymph; T.S., through part of wall of mesenteron.
7. *Ephemerella ignita;* nymph; T.S., through part of wall of ileum.
8. *Ephemerella ignita;* nymph; colon, T.S.
9. *Ephemerella ignita;* nymph; part of colon, T.S., more highly magnified.
10. *Ephemera danica;* nymph; part of colon, T.S.

PLATE VI.

FIG. 11. *Ephemerella ignita;* nymph; rectum, T.S.
12. *Leptophlebia meyeri;* nymph; part of mesenteron, T.S., showing an early stage in metamorphosis.
13. *Ephemera danica;* nymph; part of mesenteron, L.S., showing an early stage of metamorphosis.
14. *Ephemera danica;* nymph; part of mesenteron, L.S., a later stage, showing a phase of the supposed "rejuvenation."
15. *Ephemerella ignita;* nymph; part of mesenteron, L.S., showing a stage in metamorphosis.
16. *Ephemerella ignita;* subimago; mesenteron, T.S.
17. *Ephemerella ignita;* subimago; part of mesenteron, L.S.
18. *Ephemerella ignita;* subimago; part of mesenteron. A later stage.
19. *Ephemerella ignita;* subimago; part of mesenteron. A later stage.
20. *Ephemerella ignita;* ♀ imago; abdomen, T.S.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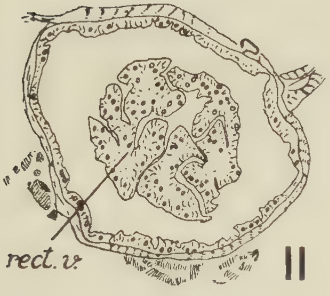
Metamorphosis of Alimentary Canal in Ephemeroptera.



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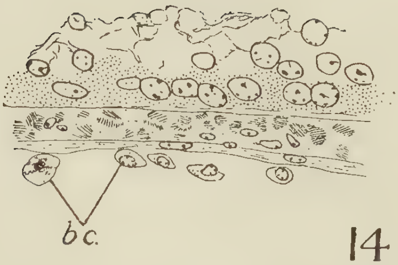

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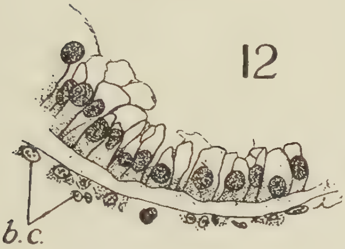

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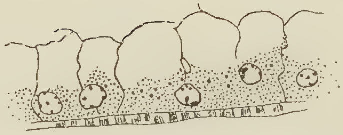

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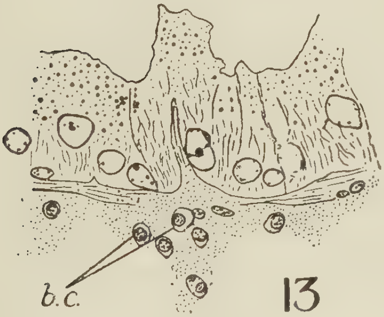

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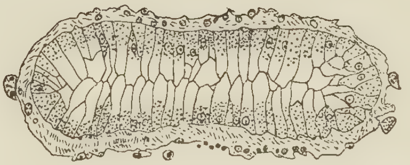

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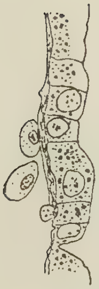

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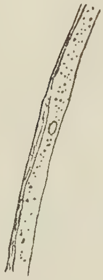

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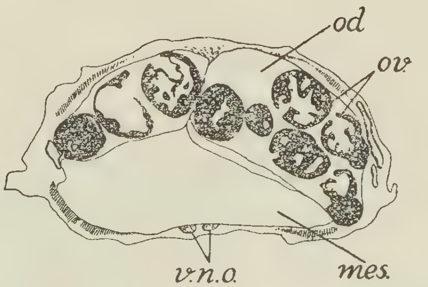
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Metamorphosis of Alimentary Canal in Ephemeroptera.

THE IMMATURE STAGES OF *PANTOPHTHALMUS TABANINUS*, THUNBERG

By Charles T. Greene.*

With

BIOLOGICAL NOTES

By F. W. Urich.†

[Read 5th November, 1930.]

Plates VII–IX.

Introduction.

This paper contains detailed descriptions of the immature stages and notes on the habits of an unusual wood-boring Dipterous larva, *Pantophthalmus tabaninus*.

In 1923 Major E. E. Austen, of the British Museum, published an interesting revisional paper on the family Pantophthalmidae (Diptera).‡ On page 556 he stated that the wood-boring habit of the larva is " unique among Diptera, so far as the present writer is aware." In America we have records in the files of the Bureau of Entomology proving that the larvae of the genus *Temnostoma*,§ family Syrphidae, bore across the grain in hard wood. Another genus having a similar habit is *Dasyllis* || in the family Asilidae, which is sometimes a secondary wood-borer. Generally the *Dasyllis* larvae follow in the galleries of the species of Cerambycidae upon which they are predators, but sometimes they bore through the wood going from one gallery to another. They are easily overlooked on account of their close resemblance to the Coleopterous larvae. The wood in which the Asilid larvae bore is not quite so hard as that attacked by *Pantophthalmus* and *Temnostoma*.

The descriptions and drawings of the egg, larva, and pupa are the work of Mr. C. T. Greene, and the biological notes that of Mr. F. W. Urich, who also presented to the U.S. National Collection all the egg and larval material from which the descriptions were prepared.

1. Descriptions.

Egg. (Pl. VIII, fig. 1.)

Large, cylindrical, dull pale olive green with the entire surface reticulate; tapering very slightly at each end with a prominent tubercle at the anterior end.

Length, 3 mm.; diameter, ·90 mm.

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* Of the Bureau of Entomology, United States Department of Agriculture, Washington, D.C., U.S.A.

† Formerly Entomologist, Department of Agriculture, St. Clair Experiment Station, Trinidad, B.W.I.

‡ " A Revision of the Family Pantophthalmidae (Diptera), with descriptions of new species and a new genus," by Major E. E. Austen, *Proc. Zool. Soc. Lond.*, **1923** : 551-598.

§ The larvae of this genus can bore a hole through solid wood as clean cut as if made by a drill.—C. T. G.

|| For one reference see 1917, *Proc. Ent. Soc. Wash.*, **19** : 149.

The eggs are arranged close together in a cluster, like a honeycomb, leaning obliquely and resting on the posterior end. When the young larvae emerge, the egg-shell splits in an irregular, longitudinal manner, leaving the tubercle intact on one side of the opening.*

Larva.

First stage, Pl. VIII, fig. 2.—Very small, pale yellowish-white, slightly more yellowish above, nearly cylindrical, tapering slightly toward the head; eleven segments in addition to the head. From the dorsum the first segment is half as long as wide; segments two to ten very narrow and all of nearly equal length; last segment as long as wide. Head is not retractile, of reddish-brown chitin, whitish along the latero-basal portion; on the antero-dorsal portion is a large, pointed, horn-like projection; back of this on the dorsum are two minute spines pointing upward; on each side, just back of this large projection, is the antenna which is small, two-jointed, thimble-like, pale yellow, length one and one-half times its diameter; palpi at anterior angle of head, reddish, slightly smaller and of the same shape as antenna; anterior spiracle small, round, reddish black, located on the side of the white area (spiracle does not show any details), between and above the antenna and spiracle is one large bristle with a small one below it; a pair of small bristles below the antenna and the spiracle. Along the dorso-central area is a longitudinal row of very short brownish bristles; on each side of this row is a parallel row of very long bristles; just below this row is a third row of large brown bristles and below this along the latero-ventral portion is a fifth row of very small bristles; last segment dorso-apically has two large, chitinised, curved, sharp-pointed, horn-like projections pointed upward and forward; on the apex of the segment, near the base of projection is a small brown bristle; on the side, at the base of and slightly longer than this horn, is a large bristle; on the latero-central portion of this segment are two very long brown bristles, the outer one much longer, the length being slightly more than the width of the larva; the lower portion of the last segment is formed like a large lower lip which can be raised or lowered and above which is a mouth-like depression; on the ventral surface of this lip are two pairs of short bristles; within this mouth-like depression on the upper half are located the posterior spiracles; † each spiracle, Pl. VIII, fig. *a*, is circular, flat, slightly chitinised and has three small, paler, circular areas on the inner half. On the lower lateral portion of the penultimate segment is one extremely long bristle which is about one and one-half times longer than the diameter of the larva. Anal opening longitudinal on venter of last segment with a broad chitinised plate on each side.

Length, 3 mm.; width, 1 mm.

Described from 15 specimens in U.S. Nat. Mus. Coll. (*F. W. Urich.*)

Full-grown larva, Pl. VIII, fig. 3.—Very large, robust, cylindrical, pale yellowish white to deep luteous; segmentation distinct. Eleven segments in addition to the head. Head very heavily chitinised, shining black, produced forward into a snout-like projection, not retractile; near the base of the head along the side are five stout bristles in a row; on the side below the centre of this row is a pair of bristles close together; along the latero-dorsal surface of head are two large bristles on each side; mandibles short, very robust, pointed apically; under surface of mandible roughened; on the outer surface of each mandible are two large bristles; along the base of the head is a transverse ventral row of short bristles, Pl. VIII, fig. *b*. The first thoracic segment is very large, heavily chitinised and for the most part a deep mahogany red; this mahogany red forms a broad, longitudinal central stripe which

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* I do not know how many eggs are generally in a cluster, but the one before me contains 63.—C. T. G.

† I find the details of the posterior spiracles especially important, since they afford very constant specific characters.—C. T. G.

continues transversely along the apical edge of the segment, the ends reaching the basal segmental line; on each side of this central stripe are three broad, tapering red stripes, slightly sinuous, extending forward and nearly touching the apical transverse red stripe; between the three red stripes are three narrow yellow parallel stripes; from the centre the first and third has a brown bristle near the base; at the apical ends and between the red stripes is a row of four brown bristles; there are three bristles below the anterior spiracle; on the side, near the base, is a prominent oval area with the broad end anterior appearing like a dark ring, the centre of which is depressed and forms the anterior spiracle, Pl. VIII, fig. *c*. In this depression are two parallel white lines connected in the middle by a small white line; the surface around these lines is granular; second segment is quite narrow, bare; third segment nearly twice as wide with a single bristle on each side on the ventro-lateral surface; the eight succeeding abdominal segments are of nearly equal width; segments two to ten without chitin. Between segments ten and eleven, attached ventrally and folded up along the sides in a depression, is a soft, delicate, smooth organ composed of several finger-like projections. This organ is apparently used for breathing when the larva is under the liquid of its burrow. The last segment is heavily chitinised, posterior surface oblique, faintly depressed in middle; near the base of the segment is a transverse row of short, raised, parallel ridges; on postero-ventral edge, in the centre, are two broad, flattened, pointed projections, below each of which is a large bristle; on each lateral edge are three brush-like groups of bristles, apparently sense-organs; transversely along the under edge of the last segment is a deep depression which may be opened or closed like a mouth; within this depression are located the posterior spiracles, Pl. VIII, fig. *d*; this spiracular plate is circular, brownish black, heavily chitinised, with a crescent-shaped slit in the middle; around this central area is a circle of 40 nearly elliptical surfaces, pale yellow with a dark slit in the middle. On each side of this lower lip are three large bristles and above these two other bristles. The anal opening is concealed under the finger-like organ.

Length, 27–32 mm.; diameter, 7–10 mm.

Described from 19 specimens in the U.S. Nat. Mus. Coll. (*F. W. Urich.*)

All the above specimens are alike in detail, differing only in size.

The above descriptions were drawn from material in alcohol; the living specimens may, therefore, be different in colour.

Pupa. (Pl. IX, fig. 4.)

Large, with shining, reddish-black head, shining mahogany-red thorax, dull luteous abdomen with truncate end.

Head: Front surface slightly oblique, covered with a number of tubercles; apex with finely marked lines; on each side of the tuberculate surface in front is a large bristle; back of this are two very robust, conical tubercles, one above the other; on the lower part of the side, near the base, are two bristles with another single one below; at the anterior basal part of head is a very large, shining black projection, bifid apically and pointed upward and outward, Pl. IX, fig. *e*. On the ventral side at the base are three large, rugose tubercles, arranged in a triangle, with two small yellow tubercles in the middle of the basal line.

Thorax smooth dorsally with numerous faintly impressed, transverse lines; antero-dorsally, along the suture are several poorly-defined tubercles; back of these is a short, transverse rugose ridge on each side; side of thorax very rugose with three or four raised, rugose areas close to the wing-pad; wing-pads smooth, shining, with faintly impressed lines arranged longitudinally; leg capsules reaching only to apex of wing-pads, their surface smooth and segmentation indistinct; anterior thoracic spiracle large, deep red, distinctly raised with a serpentine slit, composed of short, yellow, parallel lines, Pl. IX, fig. *f*; the ends of the slit are on the posterior side of the spiracular plate; posterior thoracic spiracle is somewhat elliptical with the ends of the slit on the anterior edge of the plate, Pl. IX, fig. *g*; details like those in Pl. IX, fig. *f*. The surface of the abdomen is completely covered with microscopic, red, pointed spines; each segment has a broad raised area in the middle of the side; at the upper anterior end of this surface, on each segment, is located the abdominal spiracle, Pl. IX, fig. *h*; these spiracular plates are nearly round; the first three spiracles are alike with details as in Pl. IX, fig. *f*; last three spiracles alike, small, pale luteous with the centre faintly depressed and reddish brown, Pl. IX, fig. *i*. Posterior end of pupa circular, reddish yellow, granular, with robust, long yellow bristles around the edge; central portion depressed with numerous rounded tubercles in the centre; on each side of this depressed area are two oblique, sharp ridges with stout bristles; on each side of these ridges is a faintly depressed area with a sharp transverse, oblique ridge just below the middle, Pl. IX, fig. *j*.

Length, 21–40 mm.; diameter, thorax 5–11·5 mm., abdomen 5–11·5 mm.

Described from 13 specimens in U.S. Nat. Mus. Coll.

Collected in an old trunk of Bersera at Paraiso, Canal Zone, 31st January, 1911, by Mr. August Busck.

2. Biological Notes.

Habits of the Adult Flies.

In spite of its large size and the buzzing sound it makes in flight, this large fly is rarely seen or heard. When the collector is fortunate enough, a female may be surprised during the day walking about on the trunk of a felled or standing tree, looking for a suitable place for oviposition. In this act the ovipositor is occasionally trailed along the surface of the bark of the tree. The occasions on which adults rest on trunks of trees are rare. Owing to their protective coloration these flies generally escape detection. They are also very wary when disturbed and fly away very quickly with a loud buzz. When, however, a fly is settled for ovipositing nothing will scare it, and it will not move until the last egg is laid. The mouth-parts and digestive system of both sexes are degenerate and seem incapable of being used for feeding or digestion. On the other hand, the reproductive systems are well developed, especially so in the females, which have large paired ovaries occupying almost the whole of the abdominal cavity. In an endeavour to induce copulation adults were caged with ample room for flying about. During a fortnight they made no attempt to feed on sugar and water, and eventually died through mutilating themselves in their efforts to escape. Like many wood-boring insects the adult flies vary much in size, moisture in the stem of the tree that the larvae inhabit being the determining factor.

Food Plants.

Larvae have been found boring in the following trees regardless as to whether they were standing or lying on the ground :—*Erythrina umbrosa, Ficus* sp., *Pachira aquatica*. Healthy trees are not attacked.

Life History.

Only trees dying from disease or those recently felled are attractive to the gravid female for purposes of oviposition. It is necessary that the sap of such trees be in a state of fermentation for the well-being of the larva since it is only the liquid food that is absorbed by them. The female takes advantage of any cavity or depression under the bark in depositing her eggs. She reaches such places by thrusting her ovipositor through any small hole that she may find. As a rule the side of the tree protected from wind and weather is selected. The eggs are placed close together in clusters and overlapping each other after the manner of slates on a roof. The micropylar end of the egg being always free. The clusters vary in numbers, containing anything from 50–100 eggs. In dissecting a recently-emerged female 465 fully matured eggs were counted, and there were no undeveloped ones. When first laid the eggs are of a terra-cotta colour, changing afterwards to olive green. The embryo takes 13–14 days to develop. The young larva escapes from the egg through a longitudinal slit leaving the micropyle intact. As soon as the young larvae find themselves freed of the egg-shell they crawl away. By means of their pseudopods aided by the long lateral bristles, so well figured by Mr. Greene, they are able to crawl in a vertical or horizontal direction on a moderately moist surface such as the bark of a tree. The object of this crawling about is to seek a suitable hole in the wood of the tree into which they penetrate to start their boring operations. I have not seen a young larva start boring a hole for itself, but it generally makes use of the deserted bore-holes of bark beetles of the genera *Xyleborus* or *Platypus*, which generally attack the trees before the *Pantophthalmus* larvae. Holes made by means of a small drill proved attractive to these wandering larvae. Once in a hole and after moulting, the young larva assumes the shape of the specimen figured at Pl. VIII, fig. 2. Drilling operations start, and the burrow is widened and deepened as growth proceeds. The larvae always burrow across the grain of the wood. The sides of the holes are always smooth and even, as if made by means of a sharp bit.

The actual act of boring is done by the larvae with their heads downwards and consists of a scratching and rasping operation. The margins of the burrows appear to be cut into first, and then the severed fibres of the wood are prised loose. The frass then has the appearance of short lengths of fibres, which are packed in the burrows in the shape of little wads. From time to time the frass is ejected by means of a backward movement on the part of the larvae; it is likely that the tufts of bristles on the posterior chitinous plate of the larva are used for this operation. The larvae turn easily in their burrows, and they are able to bore in a downward or upward position. They are able to close the burrows hermetically by a contraction of their bodies, the strong chitinous anal plate (Pl. VIII, fig. 2) presenting a tough surface not easily damaged by any intruding insect. The wood in which they bore and feed is generally moist, but the larvae can also bore through dry wood. A piece of white pine board, one inch thick, nailed down over some burrows was perforated right through in less than a week. The larvae will brook no obstruction in their burrows, and they must always have a clear opening into the outer world. The diameter of the holes, according to the age of the occupants, commences at 1½ mm. and ultimately becomes 10 mm. The depth to which the larvae penetrate also varies with their age, and depends to a large extent on the quantity of sap in the tree. A burrow of about 3 mm. diameter went down to 75 mm. As the larva grows, the burrows increase in depth and width, going down as much as six and nine inches according to the girth of the trunk of the tree. In no case, however, does a burrow go right through. The frass is thrown out in large quantities and forms thick layers at the base of standing trees or on the top of logs on the ground. The fermented sap of the decomposing tree is of a milky colour with an offensive odour, but there is always an abundant supply in the early stages of the decay of the tree. As the wood dries, the supply gradually lessens, and this has a marked effect on the growth of the larvae. The working of the larvae in the burrows containing much liquid causes a gurgling sound that can be heard ten or fifteen yards away from the log. The cast skins of the moults of larvae are ejected with the frass. It was not possible to ascertain the number of stages the larvae passed through during their development. The period required by the larvae to attain their full development seems to vary. It takes approximately from four to six months. When ready to pupate, the larva squares off the bottom of its burrow and carefully ejects all frass from it, leaving a perfectly clean hole. In transforming to the pupa, the larval skin splits along the dorsal side of the thorax. The cast skin is packed tightly at the base of the burrow.

The pupa cannot turn but it moves up and down in the burrow, the heavily chitinised head affording it protection against any intruders. When ready to emerge, the pupa works its body half out of the burrow, after the manner of Cossidae. The fly issues through a slit on the dorsal side of the thorax. The empty pupal cases remain sticking out of the burrows. The adult flies invariably issue after midnight and by the time the sun rises, are dry and hard enough to fly away. The period of the pupal stage seems to vary. Four weeks is the minimum period, but cases have been observed when pupae remained dormant for several months during the dry season. The total time of the development of the fly from egg to perfect stage may be summarised as follows :—

Egg stage	½ month.
Larval ,, ...	4–6 months.
Pupal ,, ...	1–6 ,,
Totals	5½–12 ,,

including an aestivating period.

From the habits of the larvae, it is obvious that this fly is of no economic importance; on the contrary, the boring into the stem helps to disintegrate the wood and make it available for plant food.

My thanks are due to Dr. S. A. Neave for revising these notes and correcting the proofs.

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EXPLANATION OF PLATES VII–IX.

PLATE VII.

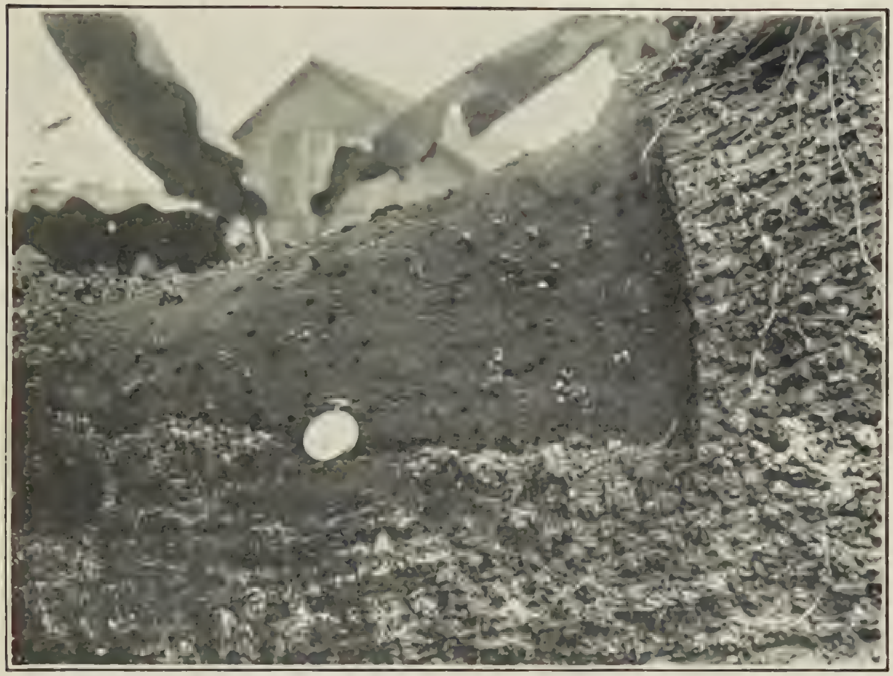
Above. Borings in log showing pupa cases.
Below. Borings in log slightly less than half natural size.

PLATE VIII.

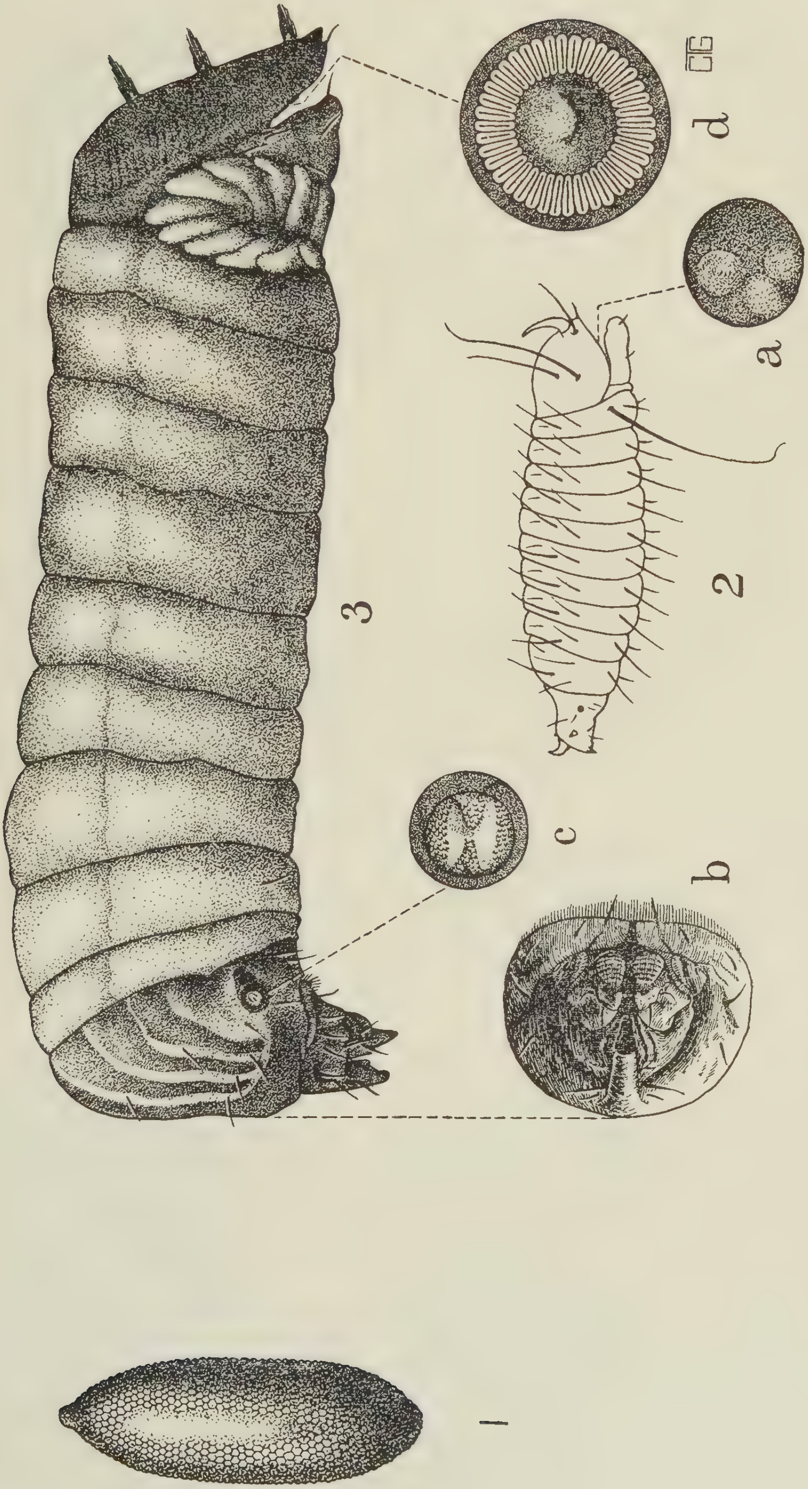
FIG. 1. Egg.
2. First-stage larva.
    a. Posterior spiracle.
3. Full-grown larva.
    b. Central view of head.
    c. Anterior spiracle.
    d. Posterior spiracle.

PLATE IX.

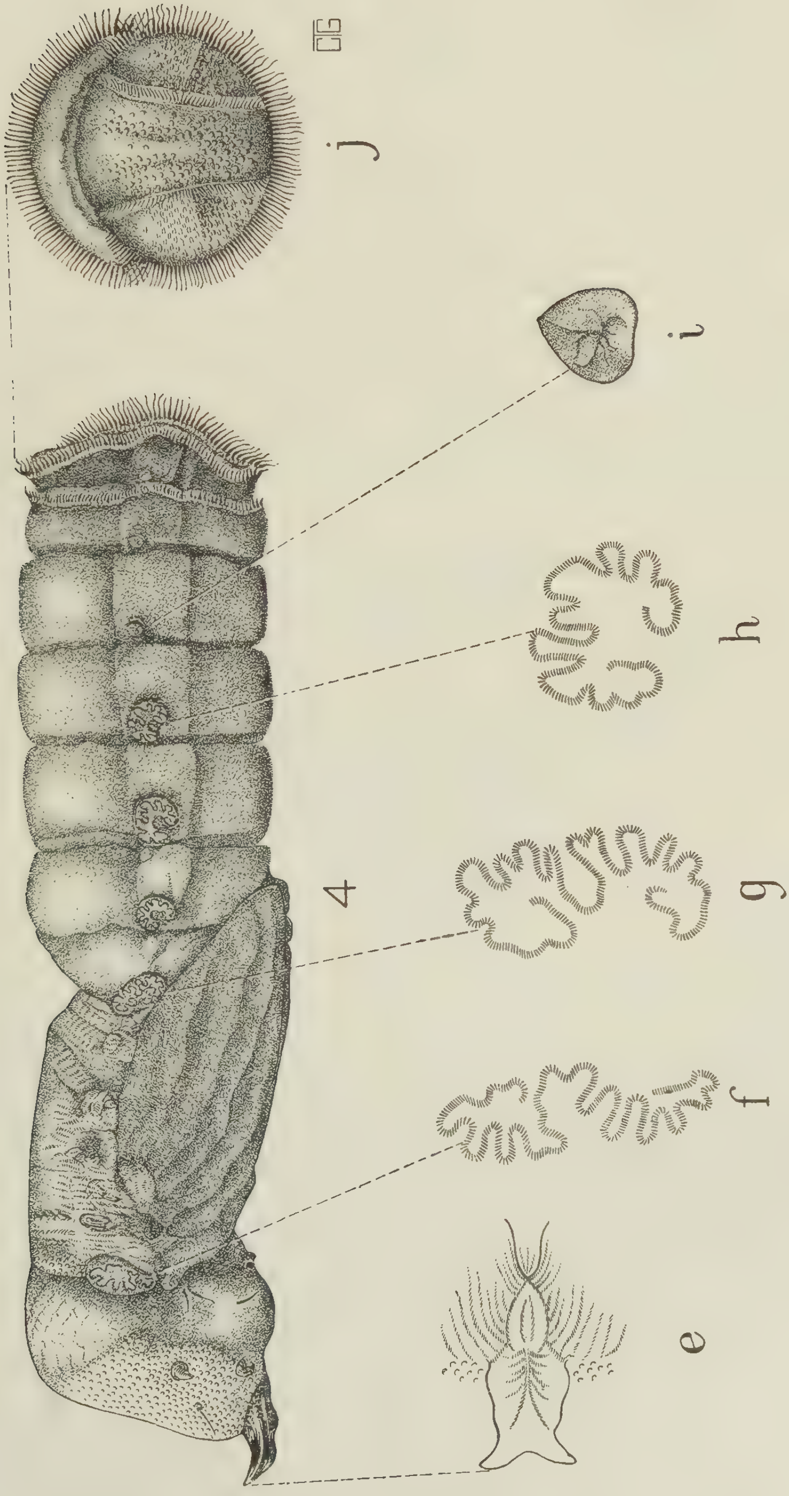
FIG. 4. Pupa.
    e. Pattern on ventral side of projection on head.
    f. Anterior thoracic spiracle.
    g. Posterior ,, ,,
    h. First abdominal ,,
    i. Last ,, ,,
    j. Posterior end of pupa.



Immature stages of *Pantophthalmus tabaninus*, Thunberg.



Immature stages of *Pantophthalmus tabaninus*, Thunberg.



Immature stages of *Pantophthalmus tabaninus* Thunberg.

OBSERVATIONS ON THE COCCIDAE OF SOUTHERN RHODESIA *

By W. J. Hall, Ph.D., B.Sc., A.R.C.Sc.

(Entomologist to the British South Africa Company in Southern Rhodesia.)

[Read 5th November, 1930.]

With Eight Text-figures.

Aonidia subsimplex, sp. n. (Fig. 1.)

Puparium of the adult female circular in outline, capsular; it consists of two plates composed of the dorsal and ventral portions of the nymphal exuviae. These plates are more or less flat, highly chitinised, and overlap the sandwiched adult female; in the earlier stages the female is entirely enclosed, but, owing to its development—more particularly in thickness—the nymphal exuviae split dorsoventrally right round the margin except for that portion covering the pygidial area. The appearance is like that of an oyster that has been partly prized open on the one side. The median longitudinal axis of the adult female usually lies at an angle of 45°–60° with that of the nymphal exuviae. Larval exuviae black, not quite central, but well within the margin. The dorsal surface of the nymphal exuviae is very shiny brown with a large shiny jet-black central area occupying at least one-half of the entire surface. Dorsal scale covered by a thin dirty-white secretionary film, which is denser over the larval exuviae and consequently makes these readily discernible. So firmly are the two portions of the nymphal exuviae attached to the adult female that it is extremely difficult to remove them. The adult female, where it has been found possible to extract it, resembles that of *Aonidiella aurantii*, Mask., in being highly chitinised in all but

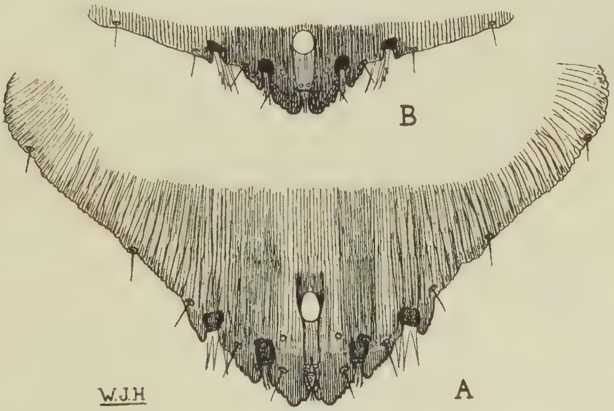


Fig. 1.—*Aonidia subsimplex*, sp. n.: A, pygidium of adult ♀, × 450; B, part of pygidium of nymph, × 450.

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* The three earlier papers of this series appeared in 1928, Bull. Ent. Res., **19**: 271–292; 1929, *loc. cit.*, **20**: 345–358, 359–376.

the pygidial region, which is delicate and retracted. That part of the dorsal scale covering the pygidium of the adult female is the thinnest and most easily fractured; it is difficult to break this away without causing damage to the pygidium of the sublying female. Diameter of puparium of adult female, 1–1·5 mm.

Male puparium smaller than that of the adult female; narrowly oval. Exuviae black or very dark, with posterior region pale brown; secretionary appendix dirty white.

Adult female with antennae represented by minute tubercles each carrying a long and a short straight seta. Parastigmatic glands wanting. Abdominal segmentation not clearly defined. No trace of tubular spinnerets at the margin of the free abdominal segments.

Pygidium triangular, retracted, with three pairs of lobes. Median pair set close together, triangular, but rounded at the apex, with a conspicuous notch on the inner edge, and 3, 4 or 5 notches on the outer edge. First pair of lateral lobes shaped like the toes of the foot, the inner or big toe being represented by a rounded projection and the remainder by a series of projections, 3–6 in number, falling away laterally. The 1st lateral lobes are very nearly as wide as the median lobes but not so long. Second lateral lobes of a similar shape to the 1st pair, but smaller, with usually only one faint notch discernible on the outer edge; in a few examples two or three notches have been faintly represented. Anal orifice relatively small, oval, situated close behind the median pair of lobes. There are two minute spiniform squamae between the median lobes, these do not extend beyond the inner notch and are difficult to discern. Two short spiniform squamae of an inconspicuous nature occur between the 1st lateral and median lobes; these not infrequently show signs of fraying at the apex. Between the 1st and 2nd lateral lobes three spiniform squamae occur. There are two marginal incisions on either side of the median lobes—one between the median and 1st lateral lobes and the other between the 1st and 2nd lateral lobes. The sides of these incisions are thickened, and the chitinous tissue not only surrounds the base of the incision but extends inwards for some distance. These chitinised areas are large and conspicuous. There is probably a marginal pore between the median lobes and one in the chitinised area at the base of each incision, but they are extremely difficult to make out with any degree of certainty. Dorsal pores are entirely absent on the pygidium and circumgenital glands are wanting.

Pygidium of the nymph very similar to that of the adult female but smaller. In this case the 2nd lateral lobes are very small and poorly represented. Anal orifice circular and very close behind the median lobes.

On *Acacia karroo*, *Acacia* spp. (Leguminosae), Umtali, 2.xii.27; Mtoroshanga Pass, Umvukwes, 16.vii.28 and 5.viii.28.

This comes close to *A. simplex*, Leon., from which it differs in the nature of the puparium and the markedly serrated form of the outer edges of the lobes. The Rhodesian species certainly differs from *A. simplex*, Leon., as recorded by Brain, a few specimens of which have been examined. Unfortunately Leonardi's original description has not been available for study.

The puparia of *subsimplex* are frequently denuded of their secretionary film, and the very shiny capsular scales, jet black in the centre shading off to brown at the margin, are then easily detected on the host-plant.

This species has been assigned for the time being to the genus *Aonidia*, but the fact that the adult female is not entirely enclosed in the nymphal exuviae strictly speaking should preclude it.

Aonidia visci, sp. n. (Fig. 2.)

Adult female entirely enclosed within the nymphal exuviae. Nymphal exuviae pyriform, relatively flat, dark reddish brown in colour and coated with a thin semi-transparent dirty-white film which extends somewhat beyond the margin. Larval exuviae similar in colour;

the thin secretionary covering is a little thicker and more conspicuous immediately above it. Nymphal exuviae highly chitinised but brittle, and it is comparatively easy to remove the extremely soft-bodied adult female from within without undue damage. Puparium of adult female: length, 1·25 mm.; breadth, 1 mm.

Male puparium relatively large, more or less parallel-sided and rounded at either extremity. Larval exuviae dark reddish brown with secretionary area a dirty semi-transparent white over the posterior third, the remainder tinged with pale brown. Length, 1·4 mm.; breadth, 0·6 mm.

Adult female broadly pyriform. Antennae represented by minute tubercles each carrying a single, very slightly curved, seta. Parastigmatic glands wanting. Abdominal segmentation hardly discernible. Margin of free abdominal segments without any tubular spinnerets.

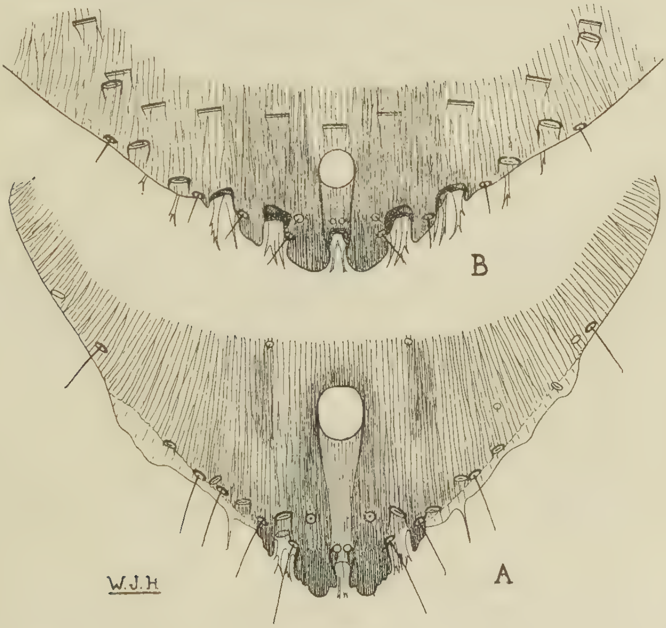


FIG. 2.—*Aonidia visci*, sp. n.: A, pygidium of adult ♀, × 900; B, part of pygidium of nymph, × 900.

Pygidium relatively small and somewhat narrowly triangular. Median lobes set close together but not touching, rounded, with a distinct notch on the inner edge and one to three notches on the outer edge. First lateral lobes very much smaller than the median pair, rounded, inner edge straight, outer edge falling away and carrying 1–3 notches. Second lateral lobes not represented. There are two minutely fringed squamae between the median lobes, these do not extend beyond the apex of the lobes. Two or three squamae, frayed towards the apex, occur between the median and 1st lateral lobes and a single spiniform squama is found beyond the lateral lobe. There are a few marginal pores on either side, and one or two pores of a similar nature just within the margin on the dorsal aspect. The anal orifice is relatively large and situated towards the apex of the pygidium. Circumgenital glands wanting.

The pygidium of the nymphal exuviae is not unlike that of the adult female. The median lobes are as wide but not so long, and, except in worn specimens, no notches are apparent. The 1st lateral lobes are similarly devoid of notches. The 2nd lateral lobes are represented by minute pointed marginal projections. In addition to the squamae found in the adult female there are two or three between the 1st and 2nd lateral lobes, the innermost of these usually approaches the spiniform type the other two being frayed on the outer edge of the apical half. There are two further squamae, frayed at the apex, beyond the 2nd lateral lobe; these are not close together and the outer one is often minute and poorly developed. The marginal pores are larger than in the adult female, and those between the median lobes, the median and 1st lateral and the 1st and 2nd lateral lobes, are surrounded by chitinous thickenings. The capitate heads of the marginal pores form a regular series at a little distance from the margin. The outermost pore on each side is situated well within the margin. Anal orifice circular, slightly smaller than the median lobes and situated close behind them.

On Mistletoe—*Viscum* sp. (Loranthaceae)—Bulawayo Park, 4.x.28, associated with a heavy infestation of *Dinaspis dentilobis*, Newst.

This is a species with well-marked characters unlike any other African species of which the description has been seen. It comes closest to *Aonidia rhusae*, Brain.

Aspidiotus (Selenaspidus) pumilus, Brain.

Brain, 1918, Bull. Ent. Res., **9** : 133.

On an unknown plant, Victoria Falls, 29.vii.29.

This has been compared with preparations from authentic specimens of the South African species and found to agree in all essential details.

Chionaspis herbae, Green.

Green, 1899, Coccidae of Ceylon, **2** : 132.

On "grass," Cataract Island, Victoria Falls, 2.viii.29. Associated with *Chionaspis stanotophri*, Cooley.

Rhodesian examples agree very well with the original description and with specimens of this species from elsewhere with which they have been compared.

Lepidosaphes mazoeensis, sp. n. (Fig. 3.)

Puparium of adult female relatively small, narrow and elongate. Larval exuviae a pale brown green. Nymphal exuviae of a similar hue, sometimes paler or even yellow at the posterior extremity. Secretionary appendix semi-transparent pale brown often with a tinge of green. Secretionary covering thin, semi-transparent, whitish. The exuviae occupy rather less than ½ of the entire length of the puparium. Ventral scale very thin, remaining adherent to the host-plant except for a very small portion round the margin. Length, 2 mm.; breadth, 0·6 mm.

Male puparium of normal form, smaller than that of the adult female, only very slightly broadened posteriorly. Larval exuviae, secretionary appendix and film similar in colour to those of the female puparium. Length, 1·1 mm.; breadth, 0·3 mm.

Adult female narrowed anteriorly, elongate pyriform, broadest across the first two free abdominal segments. Antennae represented by minute tubercles each carrying two rather stout curved bristles the one being slightly longer than the other. Anterior spiracles associated with 1–3 (usually 2) parastigmatic glands. The abdominal segmentation can be made out, but it is not well marked. Lateral margins of free abdominal segments with a few tubular spinnerets and a few aciculate gland spines. Similar spinnerets and gland spines occur on the basal thoracic segment. The median thoracic segment carries a very few spinnerets, but no gland spines, and a few spinnerets of a minute size. There is a group of a few scattered spinnerets of a similar minute form just posterior of the anterior spiracles.

Pygidium broadly rounded with a very shallow indentation apically. Median lobes slightly broader than long, rounded, very faintly but regularly serrated at the margin (except at the base) and separated by a distance rather less than the width of one of the lobes. First lateral lobes duplex, the inner lobule being much larger than the outer. Both lobules are flatly rounded and longer than broad. Second lateral lobes wanting. Squamae stout, blunted apically and sometimes obscurely bifurcated or frayed. There are two between the median lobes, which do not extend beyond the lobes, one between the median and lateral lobes, one immediately beyond the lateral lobes and two widely separated beyond with two more in addition set close together near the base of the pygidium. There is a relatively conspicuous pore carrying a tusk-like lobe between the median and the lateral lobes on each side. Marginal pores large and conspicuous, one between the median lobes and six on either side; five of these are set in marginal projections, that nearest the base of the pygidium being the largest and most conspicuous (excepting that between the median and lateral lobes). Dorsal pores scattered, with no regular arrangement, of a markedly smaller type than the marginal pores. Anal orifice slightly nearer the base than the apex of the pygidium. Circumgenital glands in 5 groups, median group 3–5, anterior laterals 7–12, posterior laterals 5–9; average of 10 examples 4 : 9 : 7.

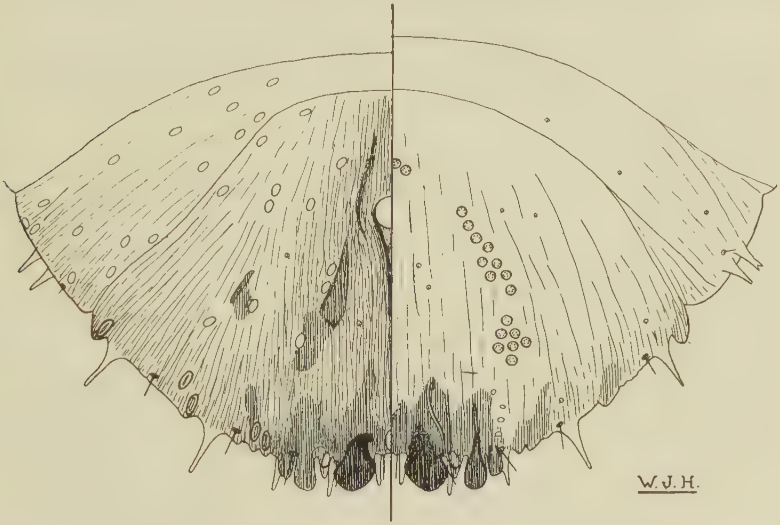


FIG. 3.—*Lepidosaphes mazoeensis*, sp. n.: pygidium of adult ♀, × 570.

On *Acacia* sp. (Leguminosae), Mazoe, 28.iii.29; on the smaller twigs and branches.

This species is unlike any other African species of the genus *Lepidosaphes* of which the description has been seen. The curious form of the squamae on the pygidium is characteristic and should serve to distinguish it easily from other allied species.

Ceroplastes.

The genus *Ceroplastes* is well represented in Southern Rhodesia. Although only a limited amount of collecting has been done, 17 distinct forms have already been found, so it is highly probable that there are a large number yet to be collected. Some of those recorded here are closely allied to previously described species from which they exhibit marked and constant, though small, differences; under the circumstances it has been deemed advisable to give these varietal rather than specific rank.

Through the kindness of Mr. Laing, all the African species of *Ceroplastes* represented in the collection of the British Museum have been examined.

KEY TO THE SPECIES OF THE GENUS *CEROPLASTES* AT PRESENT KNOWN FROM SOUTHERN RHODESIA.

A. Species in which the waxy test exhibits some conspicuous character.

1 (2). Waxy test broader than long . . . . *berliniae*, Hall.
2. Waxy test more or less circular in outline—never markedly broader than long.
3 (4). Waxy test very dark almost black . *quadrilineatus* var. *royenae*, Hall.
4. Waxy test white often with coloured markings or suffused with colour, but never uniformly dark.
5 (6). Test clearly divided into plates . . . . *rusci*, L.
6. Test not clearly divided into plates.
7 (8). With fine radiating lines of darker hue on the dome . . *toddaliae*, Hall.
8. With concentric rings of a dark hue on the dome . *zonatus*, Newst.

B. Species in which the adult female denuded of its waxy test exhibits some conspicuous character.

1 (2). Adult female broader than long . . *egbarum* var. *rhodesiensis*, Hall.
2. Adult female more or less circular or longer than broad but never broader than long.
3 (4). Margin with three bilateral and one cephalic, broad, flat and faintly bituberculate projections . . . . *ficus*, Newst.
4. Marginal outline of adult female not exhibiting singular features.
5. Caudal process of a length more than half that of the rest of the body.
6 (7). A very large species—denuded of wax 5 mm. long with caudal process 3·5 mm. long in addition . . . . *longicauda* var. *sapii*, Hall.
7. A small species—denuded of wax 2·5 mm. long with caudal process 1·5 mm. long in addition . . . . *bipartitus*, Newst.

C. Species in which the adult female under the microscope exhibits some conspicuous character.

c. Caudal process well developed, but not more than half as long as the rest of the body.

1 (2). With unusually small limbs . . . . *destructor*, Newst.
2. With limbs more or less normally developed.
3 (6). With an abnormally developed, usually bifurcated, spine associated with the stigmatic clefts.
4 (5). With cephalic and lateral tubercles well developed *uapacae* var. *chrysophylli*, Hall.
5. Without tubercles . . . . *uapacae*, Hall.
6. Without a large bifurcated spine associated with the stigmatic cleft *helichrysi* var. *sinoiae*, Hall.

cc. Caudal process rudimentary or at most represented by a small flattened conical projection.

1 (2). Limbs of adult female unusually small . *destructor* var. *brevicauda*, Hall.
2. Limbs normally developed.

3 (4). Stigmatic spines arranged in elongate loose group from the base of the stigmatic cleft inwards. Integument extremely densely chitinised and difficult to break . *berliniae* var. *enkeldoorni*, Hall.
4 (5). Stigmatic spines arranged three or four rows deep at the base of the cleft, thinning out at the margin of the shallow cleft to a single row for some distance along the margin on either side. Integument chitinised in old examples . . . . . . *rusci* var. *eugeniae*, Hall.
5. Stigmatic spines arranged in a compact triangular group at the margin of the stigmatic cleft. Integument of adult female not densely chitinised . . . . *helichrysi*, Hall.

Ceroplastes berliniae, sp. n. (Fig. 4.)

Test of adult female white, very highly convex and approximately oval in outline the short axis being the longitudinal axis of the insect. A very deep mediodorsal longitudinal depression is usually present giving a bilobed appearance. In the centre of this depression is a small, flattened, transversely striated whitish boss which often carries indications of longitudinal striations in addition. In very young individuals this boss very nearly covers the entire insect. Opercular plates black, or very dark, and sunken; in some examples this and the mediodorsal depression are continuous. The wax is soft in fresh specimens and unusually deep in relation to the size of the insect. Fusion frequently takes place where individuals are contiguous. A localised tinge of pink is seen in some specimens.

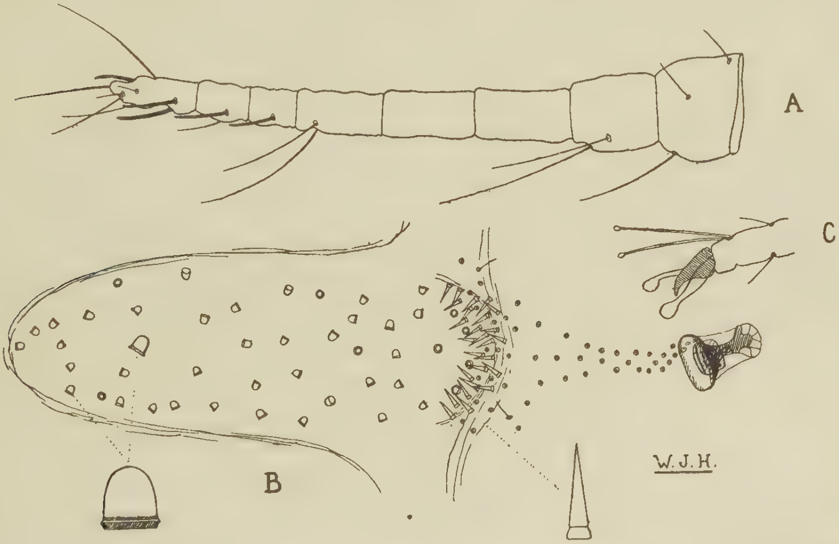


Fig. 4.—*Ceroplastes berliniae*, sp. n.: adult ♀; A, antenna, × 600; B, stigmatic spine group, × 300; C, claw and part of tarsus, much enlarged.

Denuded of its waxy test, the adult female is oval in outline, being longer than broad. The central portion is raised into a conical dome which has a tendency to be directed posteriorly. The margin is flattened and rounded, and it appears as though the central dome is set on a cushion. The cephalic lobe is comparatively well developed. Stigmatic clefts deep and conspicuous (from the under surface of the insect). A cephalic and three bilateral tubercles are present; these are small and conical, but in some specimens they are very much better developed than others. Caudal process very short, conical, with its axis at approximately an angle of 45° with that of the main body.

Dermis brown, unusually rigid and resilient, resuming its original form after pressure. All specimens prepared for microscopical examination show the dermis hyaline or at most very slightly chitinised. Length of test of adult female, 5–6·5 mm.; breadth, 8–9·5 mm.: length of adult female, 4 mm.; breadth, 2·5 mm.

Antennae of adult female usually of 8 segments; the 3rd is the longest but only very little longer than the 4th, which in its turn is very slightly longer than the 1st, 2nd, 5th and 8th. The 6th and 7th are subequal, with a tendency for the 7th to be the longer. Many examples show an incomplete division between the 4th and 5th, and in one case that between the 7th and 8th is incomplete. The 2nd and 5th each carry two long setae of unequal length. The terminal segment has a stout spine near its apex and two towards the base; the 6th and 7th each carry a stout spine which arises from about the middle of the segment. Legs normal with stout ungual, and slender tarsal, knobbed digitules. Stigmatic clefts with a group of small pointed spines arranged roughly in a semicircle around the cleft and associated with an elongate, inwardly directed, area studded with small obconical spines. One of these, situated towards the inner extremity of the area, is generally much larger than the rest. Short marginal spines present in the frontal region only; a few long setae occur on the posterior margin on either side of the anal cleft. Dermis with scattered minute tubular spinnerets, the orifices of these are set in the centre of small translucent areas which are much more apparent in some preparations than others. Caudal process very short and highly chitinised. Under the microscope the anal opercula are seen to have a large highly chitinised circumscribed area.

On *Berlinia globiflora* (Leguminosae), Mazoe, 14.viii.27; Banket, 22.ix.27; Salisbury, 4.viii.17. ex coll. Dept. of Agric. Salisbury: *Brachystegia flagristipulata* (Leguminosae), Rusape, 11.ix.27; Bromley, 5.vi.28: *Brachystegia* sp., El Dorado, 19.ix.27.

This appears to be a relatively common species on the two veldt trees quoted. The characters of the test are such that it may be at once distinguished from all other species of the genus so far collected in Southern Rhodesia. Structurally its nearest allies are *ugandae*, Newst., and *subdenudatus*, Newst.

Ceroplastes berliniae var. **enkeldoorni**, var. n.

This variety differs from typical *berliniae* in the following respects:—

1. Denuded of its waxy test the old adult female is globular, with no sign of tubercles, but with a well-developed cephalic lobe.
2. The integument of the adult female is very highly chitinised and exceptionally difficult to break.
3. Stigmatic clefts, spine groups and spines similar in every way to those found in *berliniae* but on a smaller scale.
4. Antennae of 7 segments—the 4th is the longest, with the 3rd and 7th subequal and slightly shorter; the 2nd is again slightly shorter, with the 5th and 6th subequal and the shortest.

The material was old and dried and it was impossible to make out the characters of the waxy test. There was no indication of the shape so typical of *berliniae*; the waxy test in all specimens was represented by a thin brittle white film which in many cases had been partly broken away. Diameter of the adult female denuded of wax, 2–3 mm.

On an unknown plant, Enkeldoorn, 28.x.09, ex coll. Dept. of Agric. Salisbury.

This material is certainly closely allied to *berliniae*, but if fresh specimens are collected in the future and the waxy test is not of the form typical of *berliniae*, it is probable that it should be raised to specific status.

Ceroplastes bipartitus, Newst.

Newstead, 1917, Bull. Ent. Res., **8** : 25.

On unknown plants, Inyazura, 10.vi.28, and Sinoia, 18.vii.28.

In both lots of material collected the tests were damaged and no trace of the curious marginal extensions described by Newstead could be discerned. The submarginal tubercles, also, would appear to be more highly developed. Rhodesian examples have been compared with a cotype slide in the collections of the British Museum. The cotype specimen is larger but with a relatively shorter caudal process and with relatively more spines to the stigmatic areas. In all other respects the specimens agree very well.

Ceroplastes destructor, Newst.

Newstead, 1917, Bull. Ent. Res., **8** : 26.
Brain, 1920, Bull. Ent. Res., **11** : 28.

On *Gymnosporia buxifolia* (Celastraceae), Sinoia, 18.vii.28, and *Gymnosporia* sp. Embeza, 11.iii.28 : *Citrus aurantium* (Rutaceae) Old Umtali Mission, April 1929, coll. A. Cuthbertson : *Eugenia malaccensis* (Myrtaceae), Vumba, April 1929, coll. A. Cuthbertson : and on an unknown plant, Fort Rixon, 23.vi.10, ex coll. Dept. of Agric. Salisbury.

Rhodesian examples are identical with the description of *destructor* with the exception that the adult female, denuded of wax, does show traces of lateral tubercles and is not highly chitinised as described. Also, the ungual digitules are of different form, one being of the normal type whilst the other, although approximately equal in length, is much thinner and only furnished with a small knob ; it is identical with the tarsal digitules but shorter. Newstead makes no mention of this singular feature when describing *destructor*. Specimens of *destructor* from British East Africa and Australia in the collections of the British Museum exhibit the same phenomenon and are identical in every respect with Rhodesian material.

The *Gymnosporia* shrub at Embeza was very heavily attacked and on the point of death, the branches being literally covered with this species.

Ceroplastes destructor var. **brevicauda,** var. n.

This variety differs from typical *destructor* in the following points :—

1. Denuded of wax the adult female, instead of being more or less pyriform in outline, is very nearly circular. It is very highly convex and uniformly rounded—only very slightly longer than broad. Lateral tubercles are entirely absent.
2. The caudal process is rudimentary being represented by a very small triangular projection. In *destructor* the caudal process is half as long as the body and stout.
3. In old adult females the dermis is uniformly chitinised except for a small area round the base of the caudal process. This small hyaline area is characteristic and distinguishes it at once from typical *destructor* and other allied species—with the exception of *helichrysi*.

On *Citrus aurantium* (Rutaceae), Mazoe, 1.ix.27 ; Sinoia, 17.iii.28 ; Mazoe, 5.i.28 ; Premier Estate, Umtali, 16.v.29 ; Umtali, 10.x.26, ex coll. Dept. of Agric. Salisbury : *Toddalia asiatica* (Rutaceae), Embeza, 10.ix.27 : *Cedrela toona* (Meliaceae), Umtali, 7.ix.27 ; Umtali, 21.ii.28, coll. C. H. Perrott ; Umtali, 15.iii.28 and 9.vi.28 : and on an unknown plant, Mazoe 13.xii.28.

This is the species of *Ceroplastes* commonly found on *Citrus* in Southern Rhodesia. A large amount of material has been collected, and the specimens show constant characters which enable it to be readily distinguished from typical *destructor.* The antennae, relatively very small legs, ungual digitules of unequal size and the stigmatic spine groups are exactly as found in *destructor.*

The specimen selected as " type " is an early adult female in which the tissues have not yet become chitinised.

Ceroplastes egbarum var. **rhodesiensis,** var. n.

This variety differs from typical *egbarum* (Cockerell, 1899, *Entomologist*, **32** : 127) in the following respects :—

1. Denuded of its waxy test the adult female is broader than it is long. Length, 6–7 mm. ; breadth, 9 mm.; height, 6 mm.
2. The dorsum is surmounted by a very small laterally compressed cone the apex of which presents a short but sharp edge.
3. Three bilateral tubercles are present; these are small and not very conspicuous except in smaller specimens. Cephalic tubercle not represented.
4. Cephalic lobe unusually well represented and very conspicuous.
5. The antennae are 8 segmented; the 3rd is the longest followed by the 2nd, 4th and 8th, which are subequal and only slightly shorter; the 5th is again slightly shorter, and the 6th and 7th subequal and the shortest. The individual segments are relatively wider than usual.

The unusual lateral development of the adult female is very characteristic. The width of the venter is rather less than $\frac{1}{3}$ of the total width of the adult female. Seen from the front it appears flat on top curving over and under at the sides. From the side it appears more or less uniformly rounded. In smaller examples the lateral tubercles are seen to be situated at the lower end of shallow depressions, and the integument between the tubercles is expanded into a globular prominence, two of which occur on either side. The stigmatic clefts are rather deep and conspicuous, the stigmatic spines being set in a densely chitinised area. Under the microscope the spines are seen to be of two types, those at the margin of the cleft being much longer and more pointed than those found in the main group; the latter are obconical. The cephalic lobe is very highly chitinised as is also the rudimentary caudal process which consists of a very small flat cone.

All the specimens being dried out it is impossible to give the characters of the waxy test. It must be a very large species, as the wax is obviously thick; the colour of the wax was dirty white. The tests in some cases were fused resulting in a very large amorphous waxy mass.

On an unknown plant, Bulawayo, 16.ix.21, and Hunters Road, 30.x.23, ex coll. Dept. of Agric. Salisbury.

This variety, in some respects, suggests *egbarum* var. *fulleri*, T. and W. Ckll., but the characters of the adult female denuded of its waxy test are clearly different.

Ceroplastes ficus, Newst.

C. ficus, Newstead, 1910, Bull. Ent. Res., **1** : 190.
C. pallidus, Brain, 1920, Bull. Ent. Res., **11** : 33.

On *Ochna* sp. (Ochnaceae), Banket, 16.vii.28, and *Grevillea robusta* (Proteaceae), Bulawayo, 20.x.28.

This was described originally from specimens taken on *Ficus* sp. at Bukoba on Lake Victoria Nyanza. Rhodesian examples agree perfectly with the original description and with slides of *ficus* contained in the collection of the British Museum. The outline of this species, so admirably figured by Newstead, is very characteristic and enables it to be recognised at once.

A part of the type material of *C. pallidus*, Brain, received from the Department of Agriculture, Pretoria, proved on examination to be identical with *C. ficus*. It should be noted that the antennae may be either 7- or 8-segmented. Newstead quotes the former for *ficus* and Brain the latter for *pallidus*. Rhodesian examples exhibit both 7- and 8-segmented antennae, the 4th segment of the 7-segmented antenna is the one which becomes subdivided and gives rise to 8 segments. One of the specimens of *pallidus* had 7-segmented antennae.

Ceroplastes helichrysi, sp. n. (Fig. 5.)

Test of the adult female convex and pure waxy white. There is a deep submarginal depression giving the marginal area the appearance of being rounded and thickened. The outlines of the plates are indicated by shallow depressions, and each plate carries a rather obscure median circular depression. Centre of dome with a small elongate raised white boss. There are faint indications of radiating lines and concentric rings on the dome, and a few specimens exhibited a well-marked concentric depression midway between the central boss and the submarginal groove. The wax is firm, but not hard.

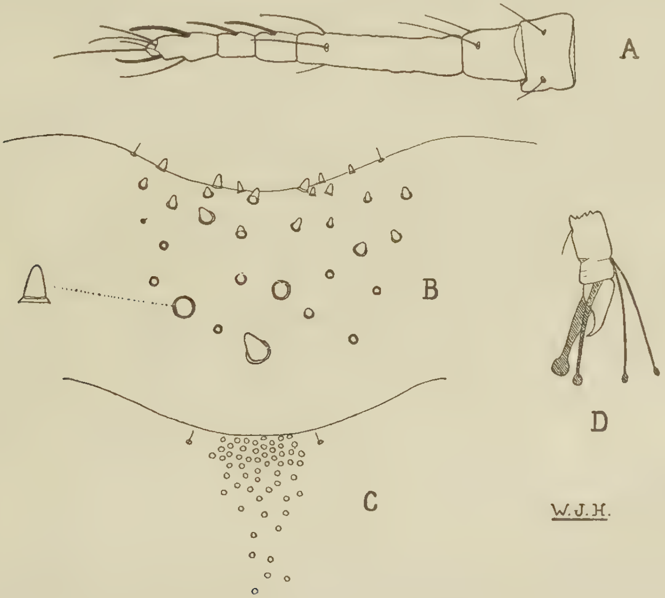


Fig. 5.—*Ceroplastes helichrysi*, sp. n.: adult ♀; A, antenna, × 450; B, stigmatic cleft and spines, × 225; C, stigmatic cleft—ventral aspect, × 225; D, claw and part of tarsus, × 675.

Denuded of its waxy test the adult female is highly convex and uniformly rounded, with a faint submarginal depression that is frequently missing in older examples. Cephalic lobe represented, but not at all conspicuous except in the younger individuals. Tubercles wanting; in a few examples there were traces of lateral tubercles. Caudal process small, triangular, with the apex directed upwards at an angle of about 45°. Stigmatic clefts shallow, but well marked. Older examples uniformly chitinised; the dermis is thin and brittle. Length of test of adult female, 5 mm.; breadth, 3·5 mm.

Antennae usually of six segments of which the 3rd is slightly longer than the 4th, 5th and 6th put together; the terminal segment carries a few stiff and bluntly pointed hairs and some of a much more slender nature. The 4th and 5th each carry one of the former, and the 1st, 2nd and 3rd one or two of the latter. In some examples a further small segment is cut off at the base of the 3rd, giving a 7-segmented antenna. Legs of normal size, but the ungual digitules are of markedly different sizes, the one being very much larger and more swollen than the other. The smaller of the two is very little stouter, and extends no further, than the tarsal digitules. Stigmatic clefts shallow. The stigmatic spines occur in a well-defined triangular group, but are relatively widely separate; they are bluntly pointed, not constricted at the base, but with a relatively large basal disc. Associated with the stigmatic spines, on the ventral aspect, is a compact group of small circular spinnerets which thins out into a straggling and intermittent series running towards the spiracles. Dorsal pores very small and relatively widely separated. Ventral dermis, opposite the caudal process, with numerous circular pores. There is a circumscribed area round the anal opercula that is hyaline and apparently free from chitin.

On *Helichrysum* sp. (Compositae), Bromley, 9.iii.28.

This species is close to *C. destructor* var. *brevicauda*, from which it differs in having limbs of normal size and relatively larger antennae; the group of stigmatic spines, also, is not so compact and covers a much larger area than in *brevicauda.*

The specimen selected as " type " is an adult female in which chitinisation has not yet set in. None of the specimens collected were densely chitinised.

Ceroplastes helichrysi var. **sinoiae,** var. n.

This variety differs from *helichrysi* in the following respects :—

1. Denuded of wax the hemispherical adult female is surmounted mediodorsally by a small but sharply-pointed spike.
2. The cephalic and three bilateral tubercles are small but relatively sharply pointed and conspicuous. They are much narrower and more sharply pointed than in any other species of *Ceroplastes* at present known from S. Rhodesia.
3. The caudal process is longer being nearly $\frac{1}{3}$ as long as the main body of the adult female.
4. The group of stigmatic spines are much smaller and more compact, made up of fewer spines of a smaller average size.
5. The ungual digitules of equal size.

On *Ficus* sp. (Moraceae)—no particulars—ex coll. Dept. of Agric. Salisbury, and on *Ficus* sp. Sinoia, 6.x.09, ex coll. Dept. of Agric. Salisbury, No. 55.

This variety can readily be separated from *helichrysi* by the nature of the adult female when denuded of its waxy test.

Ceroplastes longicauda var. **sapii,** var. n.

Unfortunately the tests of the adult female of this variety were all damaged when found. The waxy covering is thick and soft and the measurements approximated to those given for *longicauda* by Brain (1920, *Bull. Ent. Res.*, **11** : 31). No indication could be seen of the " prominent marginal area forming a wide fold at the base of the central dome."

Denuded of wax the adult female is deep brown; the measurements are much the same as for *longicauda*, and the length of the caudal process is at least ¾ that of the rest of the body. The dorsum is very highly convex and is surmounted by a small mediodorsal spike, which is rounded at the tip. The cephalic lobe is poorly represented, but there is a marked cephalic and three bilateral tubercles which are relatively small and bluntly pointed.

Under the microscope it differs from *longicauda* in :—

1. The uniform chitinisation of the integument.
2. The absence of the strange segmentation quoted for *longicauda*.

The antennae are apparently 7- or 8-segmented, but the chitinisation of the tissues makes it difficult to make them out accurately. The stigmatic cleft is much the same as in *longicauda*, being relatively small but deep. The stigmatic spines are small, thimble-shaped, widely set apart and occupying a large broadly ovate area associated with a large group of circular spinnerets. The legs are comparatively short as in *longicauda*.

On *Sapium* sp. (Euphorbiaceae), Embeza, 11.iii.28.

This large species with exceptionally long caudal process certainly bears close affinities to *longicauda*. Too much stress cannot be laid on the chitinisation of the integument (*longicauda* is said to be uniformly hyaline), but the absence of the strange segmentation clearly indicates that Rhodesian material cannot be referred to Brain's species. Unfortunately all the numerous examples collected were damaged and to a greater or less degree attacked by a fungus, but this did not preclude the characters of the female denuded of its waxy test from being readily made out.

Ceroplastes quadrilineatus var. **royenae,** var. n. (Fig. 6.)

In general appearance the tests of the adult female are identical with those of *quadrilineatus* as shown in the photograph accompanying Newstead's original description (1910, *Bull. Ent. Res.*, **1** : 193). Closer examination of Rhodesian material, however, shows that the large pyriform bodies described by Newstead are wanting. Apart from this the test of the Rhodesian species differs in the following points :—

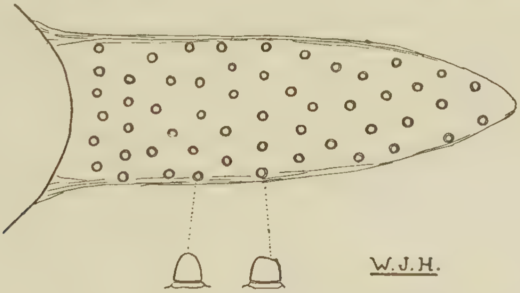


FIG. 6.—*Ceroplastes quadrilineatus* var. *royenae*, var. n. : adult ♀, stigmatic cleft and spine group, × 225.

1. The colour is very dark grey or dull black relieved only by the conspicuous white stigmatic bands.
2. The wax beneath the surface is very little paler but more transparent—certainly not white.
3. The test is extremely hard, and it is impossible to break it away without damage to the adult female. It can be loosened with xylol, which dissolves the outer layer but leaves

the remainder as a thick extremely glutinous film. Prolonged soaking in xylol will remove most of it, but a thin glutinous film remains which is very difficult to remove. Acetone was found more satisfactory in clearing away the last traces of this film.

4. The adult female as seen from the ventral aspect is brick red.

Denuded of wax the adult female differs from *quadrilineatus* in the following respects :—

1. The apex of the hemispherical dorsum is produced into a minute spike or cone which is rounded at the extreme apex.
2. Submarginal depression very deep and conspicuous; the marginal area is thickened and rounded.
3. Newstead gives no idea of the number of stigmatic spines or their arrangement. In var. *royenae* they form a well-defined elongate group running inwards from the cleft; there are no small spines interspersed although one or two are occasionally found near the outer edge of the group near the cleft.

In other respects the var. *royenae* agrees with *quadrilineatus*.—The antennae, spinnerets and spines all agree with the figures given.

On *Royena pallens* (Ebenaceae), Macheke, 11.ix.27.

This material has been compared with authentic specimens of *C. quadrilineatus* var. *simplex*, Brain, from which it differs in the arrangement of the stigmatic spines, which " are in an elongate row *around* the shallow cleft, the series becoming double in the centre."

Specimens of *quadrilineatus*, Newst., in the collection of the British Museum show the group of stigmatic spines to be under and not nearly so elongate as in the variety *royenae* and the spines are also relatively more numerous and closer together.

Ceroplastes rusci, L.

Coccus rusci, Linn., 1758, Syst. Nat. Ed. x, **1** : 456.
Ceroplastes rusci, Brain, 1920, Bull. Ent. Res., **11** : 34.

On *Ficus* sp. (Moraceae), Mazoe, 3.ii.29, and *Psorospermum febrifugum* (Guttiferae), Sinoia, 16.xii.27.

The nature of the waxy test in all examples was typical of *rusci*. Both lots of material showed slight chitinisation of the integument in the adult female and in that from *Psorospermum* the marginal and stigmatic spines were more rounded than in the material from *Ficus*, and authentic examples of this species from other countries with which they have been compared.

Ceroplastes rusci var. **eugeniae,** var. n.

Differs from *rusci* in the following characters :—

1. The waxy test in the old adult females has the plates only obscurely demarked. The submarginal line is clearly represented. The median dorsal boss is situated just below the apex of the dome on the anterior face. The smaller examples are typical of *rusci*.
2. The old adult female is very highly chitinised.
3. The stigmatic and marginal spines are larger and more numerous than in typical *rusci*, but of similar form and similarly arranged.

On *Eugenia owariensis* (Myrtaceae), Mazoe, 9.x.27 and 3.xi.27, and *Diplorrhynchus mosambicensis* (Apocynaceae), Banket, 14.xii.27.

This appears to be a well-marked variety closely allied to, but clearly distinct from, *C. rusci*, L. It comes close to *C. eucleae*, Brain—of which authentic material has been examined—but the nature of the test is different, being opaque waxy white (not a delicate green) and with a marked medio-dorsal depression carrying the usual small boss.

The specimen selected as "type" is a young adult female in which chitinisation has not yet set in and masked the characters.

Ceroplastes toddaliae, sp. n. (Fig. 7.)

Test of the adult female highly convex; the dome with a shallow median depression carrying a very small elongate boss, longitudinally orientated, rising from its base. Submarginal depression confined to a lateral indentation on either side above the stigmatic areas. The test is waxy white, often somewhat semi-transparent, and is characterised by thin radiating lines of a dark colour of indeterminate hue. These lines resemble a shaded pencil effect; they are fine, straight, close together as they leave the boss, but gradually diverge and become fainter. Diameter of test of adult female, 5–6·5 mm.

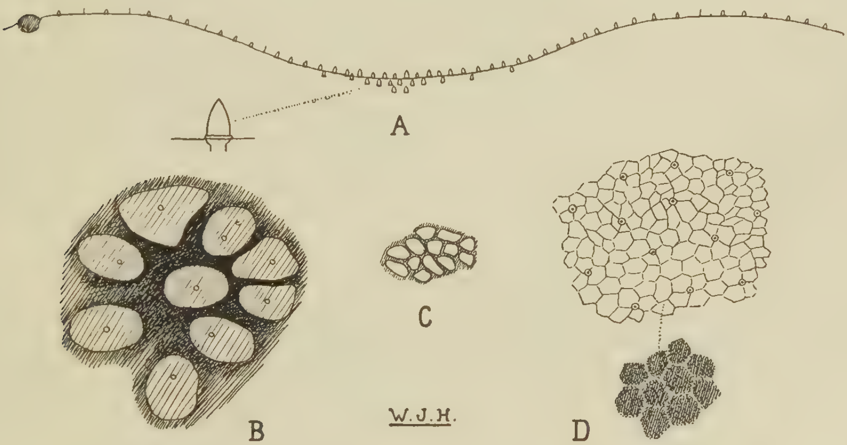


FIG. 7.—*Ceroplastes toddaliae*, sp. n.: adult ♀; A, stigmatic cleft and margin, × 150; B, honeycomb structure of the integument—large pattern—× 225; C, honeycomb structure—small pattern—× 225; D, reticulate ornamentation of the dermis and dorsal pores, much enlarged.

Denuded of wax the adult female is not very convex, but the central portion of the dermis, or dome, assumes the form of a laterally compressed cone. Submarginal area flattened with what appear to be numerous irregularly-shaped and distributed depressions of a darker colour. The marginal area is flattened with three rounded bilateral tubercles and a cephalic tubercle. These tubercles have a few faint dark marks simulating those of the submarginal region, but much less conspicuous. Beneath the extension of the integument carrying the tubercles there is a marked narrow but deep indentation separating it from the true margin, which is correspondingly flattened. Caudal process very short, triangular, directed upwards at an angle of 30°–45°. The caudal process is dark brown with a very clearly-defined circular circumscribed chitinous area in the younger examples. Stigmatic clefts shallow but well marked.

Antennae of 6 segments, the 3rd being as long as the 4th, 5th and 6th put together; of these latter the length is successively greater from the 4th to the 6th; the 2nd and 3rd segments each carry a very long seta arising from near their distal extremities. Stigmatic spines stout, pointed, somewhat swollen, but not constricted at the base. These are usually three deep at the centre thinning out to two rows, and finally a single row at the edge extending thus for some distance on either side of the cleft. Between the two clefts the spines are continuous and more or less evenly spaced. Towards the frontal and caudal regions they are replaced by short hairs of rather uneven length set at somewhat wide but regular intervals. Legs normal.

In old individuals the dermis in the vicinity of the tubercles presents a large honeycomb pattern in which the intercellular spaces are heavily chitinised. There are numerous similar honeycombed areas on a very much smaller scale, of variable size and shape, which are in all probability connected with the dark marks in the submarginal region of the adult female denuded of wax previously described. The dermis is more or less evenly studded with pores, each of which is surrounded by a small circular hyaline area; these pores are relatively widely separate, and the intervening chitinised integument exhibits a faint but clearly discernible reticulate ornamentation.

On *Toddalia austriaca* (Rutaceae), Embeza, 10.ix.27 and 11.iii.28 : *Anona senegalensis* (Anonaceae), Embeza, 30.xi.27 : *Psorospermum febrifugum* (Guttiferae), Embeza, 30.xi.27 : *Rhus* sp. (Anacardiaceae), Embeza, 10.ix.27.

The tests of all specimens collected exhibited the typical radiating lines by which it may be readily recognised. The characters are well marked and unlike any other species recorded from South Africa of which the description has been seen. The microscopic characters are suggestive of *denudatus*, Ckll., and *galeatus*, Newst., but the nature of the tests clearly indicate that they are distinct.

The "type" specimen is a young adult female in which dense chitinisation of the tissues has not yet set in.

Ceroplastes uapacae, sp. n. (Fig. 8.)

Test of the adult female pure white, relatively low convex, with a large mediodorsal depression, from the middle of which rises a minute, longitudinally orientated, elongate boss. There are no plates discernible, but usually two outgrowths of the wax on the frons and three bilaterally are present. The position of these is somewhat variable, and one or more may be missing; although small they are conspicuous, being narrowly conical, generally somewhat upturned, and tinged with red except at the tip, which is always white; there is usually also a reddish circumscribed area at the base of each prominence. In most examples these outgrowths appear to arise from shallow depressions in the waxy test. The wax is extremely soft.

Very young individuals are plum coloured with a centrally placed elongate boss, the colour immediately around which is darker. There are three white outgrowths on each side directed outwards and upwards and a similar one at the caudal extremity. Two much smaller outgrowths occur within the margin on the frons, these are divergent and not so upturned; the margin of the frons is apparent between these in the form of a crescent. Test of the adult female, in diameter, 4–6 mm.

Denuded of wax the adult female is hemispherical and uniformly rounded. Stigmatic clefts narrow but deep. No tubercles are present. Caudal process short, stout, slightly tapering and bluntly rounded at the apex. The dermis is not highly chitinised, but thin and very brittle. The pores on the dermis are small, usually tri- or quadri-locular and rather widely separate; each pore is surrounded by a narrow hyaline zone and is situated in a faintly chitinised circumscribed area. Stigmatic clefts narrow and rather deep, lined with small, but stout, pointed spines; these extend inwards to a depth of two or three rows at the base of the cleft and the spines in each row tend to be successively slightly larger away from the margin. Some distance in from the cleft, and detached from the group of spines round the cleft, is a single very large spine of variable form. It is always much larger than the largest spine associated with the cleft and may carry from one to five points. The spines extend for some distance on either side of the cleft finally giving place to some relatively short, and more or less equally spaced, simple setae. Associated with the spines of the stigmatic clefts, on the ventral aspect, is a large and compact group of pores; a few such pores occur at intervals throughout the space intervening between this group and the spiracles.

Antennae of six segments of which the 3rd is very much the longest representing nearly half the length of the entire antenna. The 4th and 5th segments are subequal and the shortest, followed by the 1st and 6th, which are subequal, and the 2nd, which is again slightly longer but less than half the length of the 3rd. The terminal segment carries a number of short stout spines and the 4th and 5th each carry one such similar spine; the 2nd and 3rd have a single very long seta which arises from a point near their distal extremities. The 3rd segment frequently shows signs of further incomplete segmentation, but only in two examples has a complete subdivision been observed; in both cases the segment cut off was a short terminal one. Legs well developed and apparently normal. The ungual digitules are of the normal swollen and knobbed type; the tarsal digitules are long, rather stouter than usual, and more conspicuously knobbed.

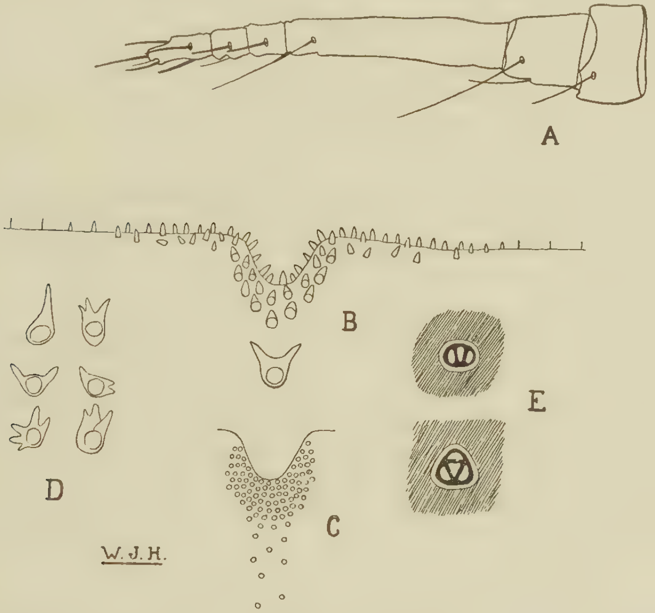


FIG. 8.—*Ceroplastes uapacae*, sp. n.: adult ♀; A, antenna, × 450; B, stigmatic cleft and spines, × 225; C, stigmatic cleft—ventral aspect, × 225; D, alternative forms of large stigmatic spine, × 225; E, two forms of dorsal pores, much enlarged.

Areas occur on the dermis, corresponding in position to the outgrowths on the waxy test, which are of an obscurely reticulate nature. The whole area is of a granular appearance under the high power of the microscope, the reticulate effect being obtained by the difference in density of the granular marking. Diameter of the adult female, denuded of its waxy test, 2·5–3·5 mm.

On *Uapaca kirkiana* (Euphorbiaceae), Mazoe, 8.x.27; the Kopje, Salisbury, 23.xi.27 and 2.iii.28, also Salisbury, 4.viii.17, ex coll. Dept. of Agric. Salisbury, No. 885: on *Eugenia malaccensis* (Myrtaceae), Umtali, April 1929, coll. A. Cuthbertson.

This species resembles *C. vinsoniodes*, Newst., in some respects, but the tests do not exhibit the remarkable star-shaped effect typical of the young adult female of that species. In addition to this the test of *uapacae* is uniformly pure white, the stigmatic clefts are deep but narrow, and the dermis apparently carries fewer spinnerets, those on the dorsum not forming an indistinct elliptic zone as in the case of *vinsoniodes*. In old adults of *uapacae* the caudal process, though admittedly small, can hardly be said to be rudimentary. It is a relatively common species on *Uapaca kirkiana* in Southern Rhodesia.

Ceroplastes uapacae var. **chrysophylli,** var. n.

Very similar to *C. uapacae*, from which it differs in the following respects :—

1. The caudal process is well developed and is usually at least half as long as the remainder of the insect. It is stout, slightly tapering and rounded at the apex.
2. Denuded of wax, the adult female exhibits a marked cephalic and three bilateral tubercles.

Apart from the above, the characters under the microscope are identical with *uapacae*. The tests of the adult female are much the same, but there are a few minor differences. The characters of the test of the variety *chrysophylli* are as follows :—

Test of the adult female white, convex, with a large deep mediodorsal depression, from the base of which arises a minute boss. The sides of the depression are generally irregularly fluted, and dirt collecting in these grooves gives sometimes a star-shaped effect. These radiating lines or grooves are developed to a greater or less degree in most specimens. Margin rounded, two lateral depressions on each side with conspicuous white stigmatic bands arising therefrom. Anal operculum set in a similar depression with a short, blunt, white, inwardly-curved filament at the margin on either side. A similar depression with two filaments, or two close together each with a single filament, inwardly directed occurs on the frons. A tingle of pale reddish brown suffuses the vicinity of each depression. The wax is relatively thick and soft.

In young individuals the reddish-brown colour is more diffuse. The white filamentous outgrowths are more conspicuous, being relatively larger. There is a single tapering truncated filament on the frons. The two bilateral filaments are continuations of the stigmatic bands and are directed upwards at such an angle that they lie relatively close to the main body of the test. The two posterior filaments are of a similar nature to the one on the frons—tapering and truncate—set wide apart and not inwardly directed. Between these two the margin is flatly rounded and in some cases is distinctly bilobed. There is only a slight tendency for the frontal and caudal filaments to be upturned.

On *Chrysophyllum argyrophyllum* (Sapotaceae), Mtoroshanga Pass, Umvukwes, 5.viii.28.

This material bears a marked resemblance to *uapacae*. The nature of the caudal process and the adult female denuded of its waxy test is sufficient to separate the two forms at once.

Ceroplastes zonatus, Newst.

Newstead, 1917, Bull. Ent. Res., **8** : 32.
Brain, 1920, Bull. Ent. Res., **11** : 35.

On *Acacia decurrens* (Leguminosae), Embeza, 10.ix.27; *Acacia woodii*, Umtali, 8.ix.27; *Acacia* spp. Greenwood Park, Salisbury, 8.iv.28, Mazoe 31.i.29

and Beatrice 30.iii.29 : on *Berlinia globiflora* (Leguminosae), Sinoia, 28.iii.28 : on *Melia azedarach* (Meliaceae), Salisbury, 8.ii.24, ex coll. Dept. of Agric. Salisbury.

Rhodesian examples agree sufficiently closely with the original description to justify assigning them to Newstead's species. The typical antenna is probably 8-segmented as described by Newstead, but it is very variable in Rhodesian material; they may have 7, 8 or 9 segments, and frequent cases of incomplete segmentation occur. The variation occurs principally in segments 4 and 5 which may be fused or, each or both, subdivided completely or incompletely.

The stigmatic areas differ in the absence of the bands of dark granular bodies between the obconical spines. In young specimens there is no trace of these, and in older specimens the entire area is densely and uniformly chitinised. The specimens on the single slide of *zonatus* in the collection of the British Museum do not show this characteristic either.

The material on *Berlinia* was identical with that from *Acacia*, with the exception that the spines of the stigmatic areas tended to be rather more pointed than obconical.

In one lot of material from *Acacia* one of the spines in the centre of the obconical spine group was much larger than the rest, and, in some cases, pointed rather than obconical. In some of the specimens from other lots of material a similar characteristic was noted, but it was less marked.

THREE RARE ABNORMALITIES IN LEPIDOPTEROUS LARVAE

HOMOEOSIS, SOMATIC MUTATION, SPIRAL SEGMENTATION

By E. A. Cockayne, D.M., F.R.C.P.

[Read 5th November, 1930.]

Plate X.

Homoeosis.

A pair of prolegs with crochets on the seventh abdominal somite.

The larva of *Brachionycha nubeculosa*, Esp., was one of a number bred from eggs laid by a female taken at Rannoch, and was sent to me on June 12th, 1930, by Mr. L. W. Newman. Unfortunately the abnormality was not detected until I had killed it for preservation. It was then full grown and few other members of the brood could be examined, but the five which I saw myself and some more looked at by Mr. Newman were normal.

The larva has a pair of small prolegs with crochets on the seventh abdominal somite, that on the right side is almost fully extruded and shows two rows of crochets, a row of nine, nearly normal in development, with their hooked tips pointing backwards and slightly inwards, and another row of eight with their tips pointing forwards and slightly outwards. Those in the second row are very irregular in size, shape, and alignment; three being very small, and one, the innermost, bifid and rough. Each row has a ridged chitinous plate in front of the hooks, that of the more perfect row being much the better developed. In the normal proleg there are about twenty-eight crochets of equal, or nearly equal, size with the hooks of all except those at the ends of the row directed inwards, and internal to them is a rectangular ridged chitinous plate. The proximal ends of the crochets are embedded in a transparent membrane, which extends beyond the crochets, but is bent sharply on itself both anteriorly and posteriorly, and is attached to the lateral aspect of the planta or extremity of the proleg on a line almost parallel, but external, to the line of attachment of the crochets. This part of the membrane becomes gradually more chitinised towards the base.

Comparing the extra proleg with a normal one, it seems probable that it became bent in the middle during development and that this part was pushed inwards towards the mid-line. This interpretation, which I owe to Mr. Hawkins, would account for the abnormal direction in which hooks and plates point, and if it were straightened out there would be a slightly imperfect proleg with seventeen crochets and a ridged plate in correct relationship with other parts. Irregular folds of membrane, transparent distally and chitinised proximally, appear to correspond with the membrane attached to the lateral aspect of the planta of a normal proleg. The extra proleg on the left side is almost completely retracted, but the tips of five crochets can be seen pointing inwards and a little backwards, the central one thicker than the others and bifid at the tip. Internal to them, part of the ridged plate can also be seen. Externally a dark triangular area shows through the skin and is probably caused by the bases of the crochets and the membrane. Both prolegs lack two of the usual three setae and the black mark, roughly triangular or quadrilateral, present on all the normal prolegs is absent. The figures show the larva twice the natural size, the external aspect of the right proleg of the fourth abdominal somite and of the right extra proleg drawn to the same scale, a ventral view of both extra prolegs, and a greatly enlarged ventral view of the crochets and plate of the right one. From the figure of the larva it will be seen that the extra prolegs must have been functionless.

The specimen is a good example of homoeosis, for the seventh abdominal somite, by the presence of a pair of prolegs with crochets, approaches in structure the third, fourth, fifth, and sixth. The fact that the prolegs are bilateral and nearly symmetrical makes it probable that the abnormality was inborn and not due to injury. It was probably not inherited, because if it had been, even as a recessive, at least two more should have been found among the remaining members of the brood. Most likely it was a new mutation.

It is generally accepted that Lepidopterous larvae formerly had a pair of prolegs on each abdominal somite like those of sawflies. Traces of those of the first abdominal somite still occur in the adult larva of *Dicranura vinula* and of *Drepana binaria* and *cultraria,* as Hawkins has pointed out, and Fracker states that hookless prolegs are found in some on the second and seventh. In the normal adult larva of *Brachionycha*, however, there is no trace of them on any of these somites, though there may be vestiges in the embryo. It is indeed almost certain that on the seventh somite structures homologous with the prolegs must be present at some stage, or there would be nothing capable of being transformed by homoeosis into prolegs. Although I have no doubt that the structures so transformed are the degraded vestiges of one pair of a series of lost prolegs, I do not think the specimen in itself affords any proof that prolegs formerly existed on this somite, but I feel sure that some will consider that it does afford such proof and will regard it as an example of atavism. In my first paper on homoeosis I gave my reasons for thinking that none of the examples of this anomaly are atavistic, and I still hold that view. Nevertheless the abnormality is a most interesting one, and I believe there is no previous record of a larva with a pair of prolegs provided with crochets situated on a somite, that is usually legless.

Cockayne, E. A. 1926, Homoeosis and Heteromorphosis in Insects. Trans. Ent. Soc. Lond., **74**: 203–230.
——. 1930, Trans. Ent. Soc. Lond., **78**: 209–226.
Fracker, S. B. 1915, Illinois Biol. Monographs, **2**, **1**: 143.
Hawkins, C. N. 1930, Proc. Ent. Soc. Lond., **5**: 26–27.

SOMATIC MUTATION.

Larva of *Cucullia umbratica*, L.

This larva was one of thirty bred from ova laid by a female taken at Eastbourne by Mr. A. J. Wightman, who very kindly sent it to me. The others were all of the usual colour, though none were quite as light as the light side of the abnormal larva. This had the head of the usual dark brown colour with faint orange stripes, but the rest of the larva was sharply divided down the middle line into a left half of the usual colour, dull orange brown with indistinct and incomplete dark brown longitudinal stripes, and a right half which was almost entirely blackish brown. The ground-colour on this side was, however, visible as a fairly distinct lateral stripe of dull orange on the thoracic and on the ninth and tenth abdominal somites, and on the anal plate the right half of the central orange stripe was present but much encroached upon by the black pigment of the outer part. The prolegs had the usual conspicuous pale dot on the outer aspect. During life the contrast between the two halves was very striking, though the difference is exaggerated in the figure by the orange ground-colour being left white. The larva was in its penultimate instar, when it died on September 11th, 1929. I was unable to find a testis on either side, and think that both sides were female.

Larvae with irregular mosaics of two distinct colours or patterns or with one half of one colour or pattern and the other of a different one have been described in *Bombyx mori*, but those bred have proved to be gynandromorphs. If this larva was female on both sides, gynandromorphism can be excluded and it falls into the group of somatic mosaics.

Some years ago I published lists of those recorded in Lepidoptera, and in many of them the colour or pattern of one side was known to be dominant or recessive to that of the other. Only one larva was included, a *Chaerocampa elpenor*, brown on one side and green on the other, and both pupa and imago also differed in colour on the two sides. Federley tried to work out the inheritance of green and brown in this species, and at first suspected that green was recessive, because he had a brood of 42 brown and 10 green larvae, but in the next generation green × green gave 73 brown larvae, green × brown gave 158 brown, and brown × brown, 56 brown. From this he concluded that green and brown were genetically identical. Another observation appears to confirm this, for in some localities the majority of larvae found wild in their last instar are green, but larvae taken young and kept in captivity almost invariably turn brown. The mosaic, however, must have been genetically different on the two sides. Presumably a bias towards green or brown is inherited, but it can be overcome by environment.

The larvae of *umbratica* vary considerably; some are lighter than the light side of the mosaic and two bred from eggs this year were very nearly as dark as its dark side. It is not known whether the variation is entirely due to inherited factors or in part due to environment.

Morgan in his "Origin of Gynandromorphs" discusses somatic mosaics and says that there are three possible ways in which they might arise: by the fertilisation of a binucleate ovum, by a mutation occurring in one of the chromosomes of a somatic cell, or by the elimination of an autosomal chromosome at or after the first division of the fertilised ovum. He thinks the last unlikely, because there is no evidence that an animal can survive the loss of an autosomal chromosome, though it is proved that the loss of a sex chromosome is one of the causes of gynandromorphism. Fertilisation of a binucleate ovum by two spermatozoa is known to happen and would result in the production of a somatic mosaic, if each carried a different gene for colour and both were male or female-determining; in such a case, however, one would expect to find amongst the other members of the brood some with the same colour or pattern as the one half of the mosaic and others with that of the other half. In this case none of the other twenty-nine larvae resembled the blackish-brown side of the mosaic. The third way appears to be the most probable, and, if the mutation occurred just after the first division of the ovum and were one affecting larval coloration, a larva like this *umbratica* would be produced.

In *Drosophila* all the ten mosaics mentioned by Morgan were males and in nine of them one part of the mosaic resembled a mutation previously known to be a sex-linked recessive. These two facts are important, for a recessive mutation affecting only one chromosome cannot show any external sign unless it has occurred in the X-chromosome and in the sex having only a single X-chromosome, which in *Drosophila* is the male. Occurring in an autosomal chromosome it would be rendered invisible by the dominant allelomorph in the corresponding autosome, and in the X-chromosome of the female by that in the other X-chromosome. This is greatly in favour of all these mosaics being somatic mutations, and in the case of some of them there is other evidence pointing to the same conclusion.

In Lepidoptera on the other hand the female has the unpaired sex chromosome, and a recessive somatic mutation will only be recognisable in the female. Therefore, if mosaics in this Order are of the same nature as those in Diptera, we should expect the majority to be female, since the dominant mutations will be manifest in either sex, but the recessive ones in females only. In the lists of somatic mosaics which I have published in the *Entomologist's Record* we find if the more doubtful ones are excluded, thirty-one in females, or thirty-two including the *umbratica*, and sixteen in males. No preponderance of females would be expected if they arose from binucleate ova or by the elimination of an autosomal chromosome. It is therefore probable that most of these mosaics arose by somatic mutation.

In Coleoptera Breitenbacher working on the inheritance of elytral colour in *Bruchus quadrimaculatus*, Fabr., discovered forty-eight mosaics. All were females and the abnormality of colour affected one elytron only. In every case this elytron showed a colour that was dominant, sex-limited to the female, and due to a gene in an autosomal chromosome, and all the progeny of those kept for breeding purposes were recessive like the major part of the parent. Breitenbacher says that they cannot have arisen from binucleate ova, because only one elytron was affected and not half the insect, nor can they have resulted from the elimination of an X-chromosome, because the colour was due to a gene in an autosome. He dismisses the elimination of an autosome as most unlikely, and considers that they were dominant somatic mutations.

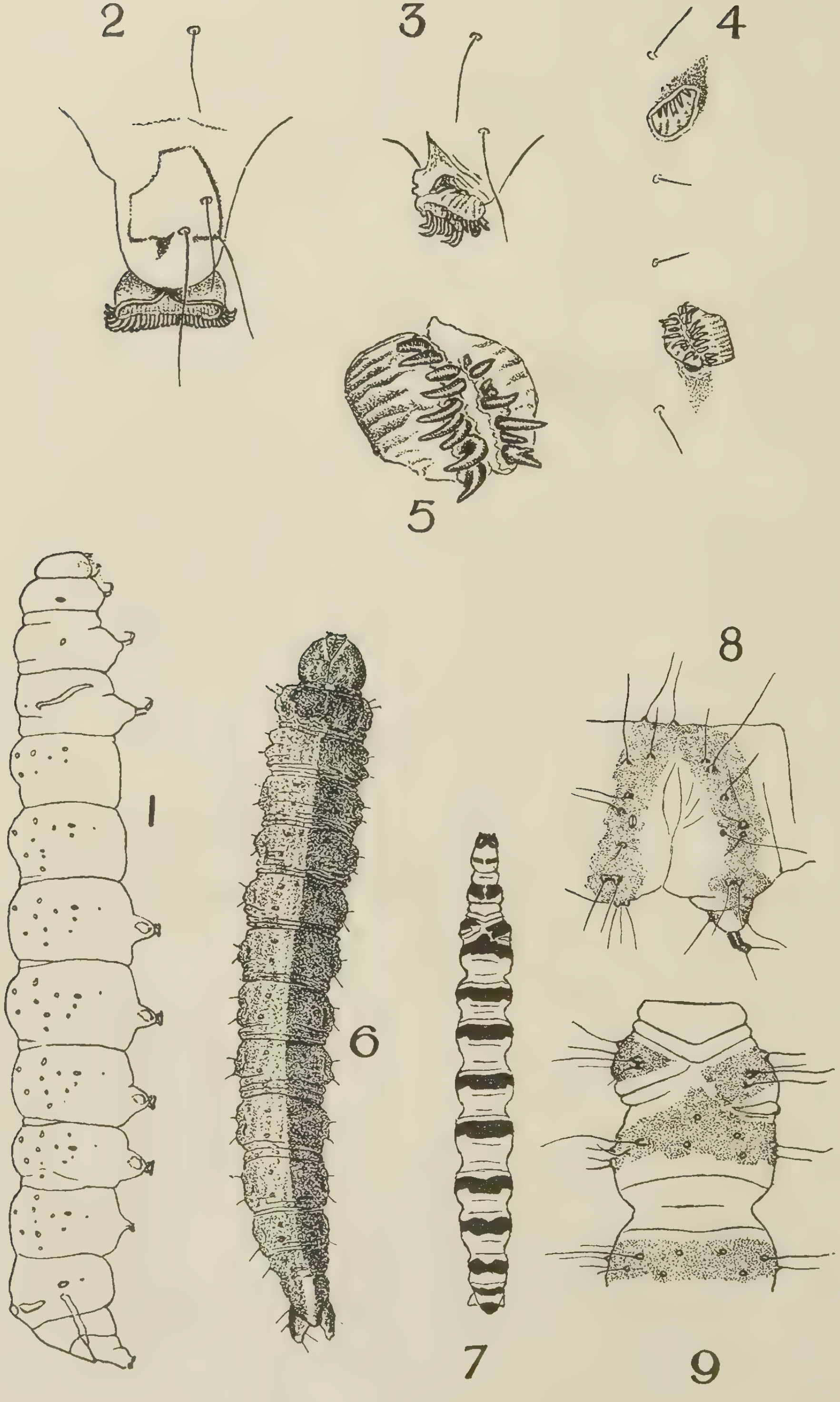
Thus the evidence derived from Diptera, Lepidoptera, and Coleoptera alike supports the view that somatic mosaics are generally due to mutations occurring in one of the chromosomes of a nucleus in the somatic tissues, and, though there is evidence that some in Lepidoptera arise from binucleate ova, there is little doubt that even in this Order the origin of the majority is by mutation.

Breitenbacher, J. K. 1922, Biol. Bull., **43**: 10–22.
Cockayne, E. A. 1922, Ent. Rec., **34**: 105–118, 200–1.
——. 1924, *loc. cit.*, **36**: 17–20.
——. 1928, *loc. cit.*, **40**: 17–21.
Federley, H. 1916, Öfvers. Finsk. Vetensk.-Soc. Förhand., **58**: 1–13.
Morgan, T. H., and Bridges, C. B. 1919, Origin of Gynandromorphs. Pub. Carnegie Inst. Wash., **278**: 27–33.

SPIRAL SEGMENTATION.

Larva of *Hipocrita jacobaeae*, L.

This was found by Mr. C. N. Hawkins, when we were at Chalfont St. Giles on July 10th, 1930, and was very kindly given to me. The spiral is dorsal and begins on the left side of the metathorax. The right half of the metathoracic somite is united dorsally to the left half of the first abdominal, and



Abnormal Lepidopterous larvae

the spiral ends on the right side of the first abdominal, but the separation of the two halves of this somite is incomplete. All the setae are present on the two abnormal somites; those of the metathorax are but slightly displaced, but setae 1 and 2 on both sides of the first abdominal are so much displaced to the right that in the lateral view both pairs are visible. This somite and all the succeeding ones are twisted over a little to the right. The exact arrangement of the spiral and of the setae is shown in the drawings made from the dried skin and needs no further description. This is only the second example of a spiral in an insect involving the thorax, and the first to be recorded in a lepidopterous larva. It is, however, not the first spiral in this species. Last year I gave a figure of the larva of *jacobaeae* in the British Museum, and I believe one or two others with spiral segmentation were recorded some years ago, but have been unable to trace the reference.

Cockayne, E. A. 1929, Spiral and other anomalous forms of segmentation, Trans. Ent. Soc. Lond., 77 : 177–184. (Bibliography.)

Explanation of Plate X.

Fig. 1. Larva of *Brachionycha nubeculosa* with extra pair of prolegs (× 2).
2. External aspect of right proleg of fourth abdominal somite.
3. External aspect of right extra proleg (same magnification).
4. Ventral view of both extra prolegs.
5. Ventral view of crochets and plates of right extra proleg.
6. Larva of *Cucullia umbratica*, somatic mutation (× 4).
7. Larva of *Hipocrita jacobaeae* with spiral segmentation (× 2).
8. Right side of metathorax and first abdominal somite (× 6).
9. Dorsum of metathorax and first and second abdominal somites (× 6).

ON SOME MORDELLIDAE FROM NEW GUINEA AND FIJI

By ARTHUR M. LEA.

[Read 5th November, 1930.]

WITH TWO TEXT-FIGURES.

COMPARATIVELY few species of MORDELLIDAE have been recorded from New Guinea, but as Mr. C. T. McNamara obtained no less than 25 species (several of these have been left unnamed as they are represented by single specimens without conspicuous markings) in a few months at Mount Lamington alone, it is probable that the family is as abundantly represented there as in the Cairns district of Queensland, where many of the species have only been obtained from flowers on the tops of tall trees.

Some of the New Guinea forms appear to be but slight varieties of Queensland species, and several extend to Fiji and elsewhere in the Pacific.

NEW GUINEA.

Mordella incisura, sp. n.

Black, brilliantly iridescent, elytra brownish flavous, the suture narrowly and sides more widely blackish, front femora partly pale. With blackish and whitish pubescence.

Antennae moderately long, fourth to tenth joints dilated to apex. Pygidium the length of hind tarsi, acutely ridged along middle and conspicuously notched at apex, which is fringed with black bristles. Spurs to hind tibiae comparatively short, one slightly longer than the other. Length, 12–13 mm.

NEW GUINEA: Wareo, Finsch Haven district (*Rev. L. Wagner*); N.E. PAPUA: Mount Lamington, 1300–1500 ft. (*C. T. McNamara*).

A large narrow species structurally close to *M. elongatula*, but with very different markings, elytra mostly pale and pygidium conspicuously notched. Possibly a new genus should have been proposed for it. The iridescence of the head is very brilliant on fresh specimens, has an arched appearance and is rainbow coloured; in most places it is bluish, becoming purplish on the hind coxae. The whitish pubescence is fairly dense on parts of the head and becomes yellowish in front; on the prothorax it margins the base and sides, and from the base forms two vittae that extend forwards till they meet or almost meet an oblique vitta from each front angle; it is dense and snowy on the scutellum; on the elytra it is rather sparse on the shoulders and suture and forms two feeble fasciae, one before and one behind the middle; on the legs and parts of the under surface it is fairly dense.

Mordella biauronotata, sp. n.

Black. Clothed with black and white pubescence, and with two large, round, orange-coloured spots on elytra.

Antennae rather short, some of the joints slightly transverse. Pygidium moderately long and rather sharply pointed. Spurs to hind tibiae black and subequal. Length, 4–5 mm.

Papua : Mount Lamington (*C. T. McNamara*). Two specimens.

A rather robust species, very distinct from all others before me by the two large orange spots on elytra; these are at about the apical third and touch the suture and sides. The white pubescence is fairly dense on the head, but alters in appearance with the point of view; on the pronotum it distinctly margins the base and forms a narrow but not complete fascia across the apical third, connected with a short vitta on each side of middle; the scutellum is entirely clothed with it; on the elytra it is confined to less than half of the suture at the base; it clothes the metasternal episterna (on each of these from some directions it appears brightly silvered, from others opaque), outer basal angles of hind coxae, and of each of the four basal segments of abdomen, the base of the pygidium and on parts of the legs.

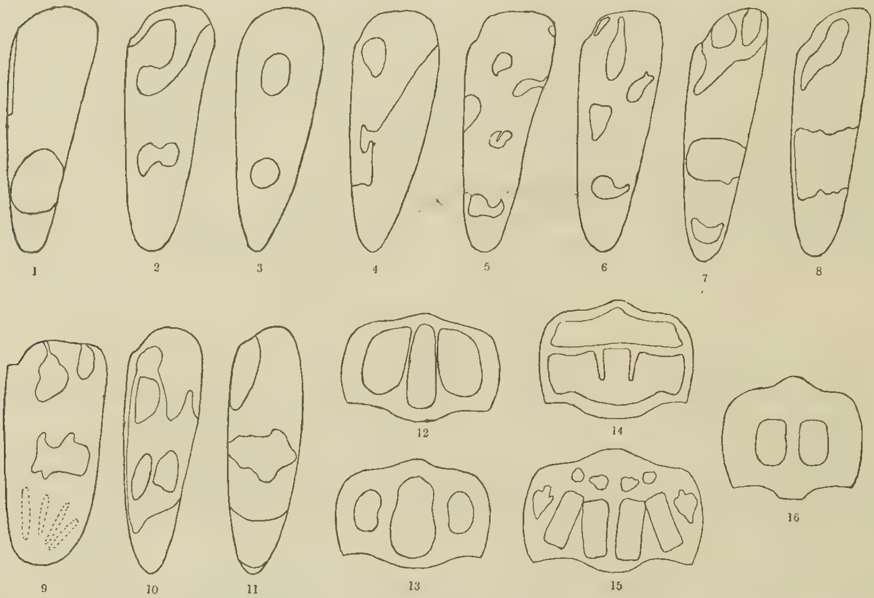


Fig. 1.—Markings of right elytron of *Mordella biauronotata*, Lea; 2. of *M. mcnamarae*, Lea; 3. of *M. tetraleucosticta*, Lea; 4. of *M. vicina*, Lea; 5. of *M. decemguttata*, Fab.; 6. of *M. leucospila*, Fairm.; 7. and 8. of *M. elongatula*, Macl. var.; 9. of *Tomoxia oblongifera*, Lea; 10. of *Mordellistena epicallens*, Lea; 11. of *M. bimaculicollis*, Lea; 12. Prothoracic markings of *Mordella mcnamarae*, Lea; 13. of *M. tetraleucosticta*, Lea; 14. of *M. leucospila*, Fairm.; 15. of *Tomoxia oblongifera*, Lea; 16. of *Mordellistena bimaculicollis*, Lea.

Mordella mcnamarae, sp. n.

Black, in parts iridescent, parts of antennae and of front legs obscurely reddish. Clothed with black and white pubescence.

Antennae rather short. Pygidium rapidly narrowed to apex, but tip truncated. Spurs to hind tibiae comparatively short and subequal. Length, 6–8 mm.

Papua : Mount Lamington (*C. T. McNamara*). Three specimens.

A rather robust species, structurally fairly close to *M. hamatilis*, but larger, and elytra without apical markings. The tip of the pygidium is truncated, but as the scutellum does not abruptly cut into the elytra, the species was not referred to *Tomoxia*. The white pubescence is fairly dense on the head; on the pronotum it covers all the margins, and forms a narrow vitta on each side of the middle, so that three large black spots are left; it clothes the scutellum and a space adjacent to it on each elytron; each shoulder is clothed, and the mark is curved round and dilated to near the suture at the basal third; there is also an isolated transverse spot just beyond the middle, and almost touching the suture and side, the base of the pygidium, parts of the legs and much of the under surface.

Mordella tetraleucosticta, sp. n.

Black, in parts brilliantly iridescent. Clothed with black and white pubescence.

Antennae not very long, second and third joints short. Pygidium long and thin. Spurs to hind tibiae pale brownish and very unequal, the longer fully half the length of the first tarsal joint. Length, 6 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Unique.

In the Queensland *M. metasternalis*, which sometimes, owing to partial abrasion, appears to have the elytra with but four spots, the derm beneath the spots is black; in the present species the derm beneath them is whitish. *M. tetrastictoptera* is a narrower species, with dingier clothing and shorter pygidium. The white is rather sparse on the head, narrowly margins the base of the pronotum, from some directions is conspicuous on the scutellum, forms four spots on the elytra, small spots on the under surface, is conspicuous at base of pygidium, and sparse on the legs. Of the spots on each elytron the first is at the basal third in the middle, and the second is in line with it at the apical third.

Mordella incisa, sp. n.

Black. Clothed with black and whitish-grey pubescence.

Antennae rather short and thin. Pygidium short and obtusely pointed. Spurs to hind tibiae moderately long, blackish and unequal. Length, 3 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Unique.

A small species, with a notch in the clothing of each elytron much as in many specimens of *M. limbata*, but with a much shorter pygidium; almost as on a *Tomoxia*, but the scutellum has the sides rounded and not angularly cutting into the elytra. The pale pubescence is almost uniform on the head, clothes the pronotum except for a large median subovate spot, and a smaller one towards each side; on the elytra its outer edge runs obliquely backwards to a distinct notch at the middle, is then dilated and abruptly terminates at about one-fourth from the apex, but there is also a black spot on each side near the scutellum, the undersurface and legs are also partly clothed with whitish-grey pubescence.

Mordella leucopleura, sp. n.

Black, parts of upper surface brilliantly iridescent. Clothing mostly black.

Antennae not very long, fifth to tenth joints serrated. Pygidium rather thin, about as long as hind tarsi. Spurs to hind tibiae blackish, unequal, the longer not half the length of the first tarsal joint. Length, 6 mm.

NEW GUINEA: Wareo (*Rev. L. Wagner*). Unique.

A rather narrow, deep black species. *M. nigrans*, from Queensland, is smaller, the scutellum without white pubescence, or, if with such, the prothorax with narrow pale markings. Some of the darker varieties of *M. baldiensis* have whitish clothing on the scutellum, but the pygidium is different. *M. corvina* is smaller and more compact, with a shorter pygidium. The only white pubescence on the upper surface is on the scutellum, but there is some greyish pubescence on the muzzle, and very sparse about the base of the pronotum. There is some white pubescence at the base of the pygidium, on the metasternal episterna, base of each abdominal segment (dilated to each side) outer base of hind coxae, and on parts of the femora; from some points of view it appears brilliantly silvered, but from others opaque.

Mordella decemguttata, Fab.

A specimen from Mount Lamington, evidently belonging to this species, measures 13 mm. in length, including the pygidium.

Mordella leucospila, Fairm.

Twelve specimens from Mount Lamington, evidently belonging to this species, vary in length from 8 to 12 mm. (including the pygidium), and, except for slight variations, have constant markings.

Mordella octomaculata, Macl.

Numerous specimens from Mount Lamington and Finsch Haven agree with Queensland specimens of this species. On an occasional one the two sub-basal spots (one submedian the other subhumeral) are conjoined so that the elytra appear to have but six spots. On some of the smaller specimens the subhumeral spot is almost absent.

Mordella elongatula, Macl.

Numerous specimens from Mount Lamington and Finsch Haven appear to represent a slight variety of this species. They appear to agree with Fairmaire's description * of *M. textilis*, Montr. If correct, Montrouzier's name has precedence.

Tomoxia oblongifera, sp. n.

Black, parts of front and of middle legs obscurely reddish. Clothed with black and whitish pubescence.

Antennae short and rather thin. Scutellum short and transversely suboblong, the sides abruptly cutting into elytra. Pygidium not much longer than wide, tip truncated. Spurs to hind tibiae almost flavous and unequal, tarsi comparatively short. Length, 3 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Unique.

Unusually short and robust even for *Tomoxia*, and with a very short pygidium; the prothoracic markings should also be distinctive. The clothing on the head is white and longitudinally parted in the middle. On the pronotum there are twelve black spots or marks, four small round ones in front, two small irregular ones on each side, and four narrow oblongs in pairs, each pair almost touching in front (slightly in advance of the middle) and widely separated behind (close to the base). On each elytron the black markings consist of two fairly large basal spots, of which one is humeral, a large irregular median spot, and four ill-defined vittae towards the apex. On the under surface and legs the clothing is mostly whitish.

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* Fairm., 1887, *Ann. Soc. ent. Belg.*, 26.31.

Tomoxia suboblongifera, sp. n.

Black, parts of antennae and of front legs obscurely paler. Clothed with black and white or whitish pubescence.

Antennae, scutellum, and pygidium much as on preceding species. Spurs to hind tibiae black and unequal, the longer not half the length of the following joint; basal joint of hind tarsi almost twice the length of the following one, the two combined distinctly longer than tibiae. Length, 3·5–3·7 mm.

PAPUA: Mount Lamington (*C. T. McNamara*).

Fairly close to the preceding species and similarly robust, but larger, with more diffused markings, hind tarsi distinctly longer (the basal joint very distinctly so), and spurs to hind tibiae blackish and shorter. The whitish pubescence has a median parting, but is fairly uniform on the head; on the rest of the upper surface, it occupies much less than half the surface and has a straggling appearance, the markings being thin and ill-defined; on the pronotum there is a curvilinear triangular white spot on each side of the base and a thin median line; on one specimen four feebly defined suboblong black patches may be traced, but on a second one even these are not traceable; on each elytron a narrow interrupted white line may be traced near the suture and faint remnants of other markings. The white markings of the sterna, hind coxae, and abdomen are as in many species of the family, but are rather ill-defined; the pygidium has a white patch at the base, and a less defined apical one.

Mordellistena epicallens, sp. n.

Dark brown, parts of elytra, abdomen, antennae, palpi and legs reddish-brown. Clothed with pale (but not white) pubescence, uniform on most parts but forming a pattern on elytra.

Antennae front and middle legs long and thin. Pygidium long, thin and acutely pointed. Hind tibiae with three long and one short, oblique black ridges, spurs unequal, the longer one about twice the length of the other; first joint of tarsi with four ridges, second and third each with three. Length, 4·5 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Unique.

Very distinct from any previously described New Guinea species, but close to the Fijian *M. inscripta.* On the pronotum three slightly darker spots are vaguely indicated; but on each elytron the darker markings are distinct and consist of a subscutellar spot, a jagged antemedian fascia and a jagged postmedian one, the antemedian fascia connected with each of the other markings by two narrow vittae, as a result there are five isolated paler spots, beneath which the derm is also paler than beneath the dark markings.

Mordellistena majorina, sp. n.

Black, slightly iridescent, antennae and parts of legs obscurely paler. Almost uniformly clothed with dark pubescence.

Antennae long and thin, fourth to tenth joints feebly serrated. Pygidium long, thin, and acutely pointed. Hind tibiae with five ridges, of which three are long and distinct, one is short and apical, and the other is sub-basal and inconspicuous from most directions, although sufficiently distinct from others; spurs obscurely reddish and rather long, the shorter about the length of the second tarsal joint, the other distinctly longer, first joint of tarsi with three long ridges, second and third each with two rather inconspicuous ones. Length, 10 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Unique.

Larger than any other species of the genus before me. From most directions the entire clothing appears to be quite as dark as its supporting derm, but from others it has a slightly speckled appearance, becoming almost uniformly white on the scutellum.

Mordellistena cryptomela, sp. n.

Pale castaneous, mesosternum, metasternum, hind coxae (except about middle) and sides of elytra on basal half (invisible from above) blackish brown; pygidium and rest of hind legs paler, but much darker than the other legs. Uniformly clothed with silken pubescence, except that on the dark parts it is also dark.

Antennae thin, four basal joints rather short, the others longer, eleventh longest of all. Pygidium not thrice as long as the basal width, apex acute. Front legs thin, middle legs also thin but much longer; hind tibiae with very unequal spurs, the longer more than half the length of the following joint. Length, 5·5–7·5 mm.

PAPUA: Mount Lamington (*C. T. McNamara*).

Paler and considerably larger than *M. dodoneae.* Five specimens were obtained; of these two are larger than the others and are evidently females; the smaller ones are certainly males (their genitalia are protruding). Their colours and clothing are practically identical, and I believe they belong to but one species. The females, however, have three long black ridges, and one short one, on the hind tibiae, the first joint of the tarsi has four and the second and third two each. On the males the ridges are three on the tibiae, and three, two and two on the tarsi.

The fact that the setose ridges on the tibiae are sexually variable in this species is a somewhat disturbing feature, as they have been generally regarded as constant in each species of the genus.

Mordellistena egregria, sp. n.

Black, parts of abdomen brilliantly iridescent; head pronotum and scutellum bright reddish flavous, middle of abdomen, base of antennae, middle and hind tarsi and spurs flavous, trochanters and front tarsi somewhat darker. Pubescence of upper surface pale on the pale parts, and black on the black, but whitish on much of the under surface and legs.

Antennae rather long and thin. Hind tibiae with four long setose ridges and a short apical one, spurs very unequal, the longer one almost as long as the basal joint of tarsi, this with four setose ridges, the second with two. Length (to apex of elytra), 5 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Unique.

A moderately large, distinctively coloured species, fairly close to the Queensland *M. erythroderes*, but the head is no darker than the prothorax and the hind tibiae are different. The shoulders are obscurely reddish. The pygidium is missing from the type.

Mordellistena iridipennis, sp. n.

Reddish-castaneous, elytra black and brilliantly iridescent. Clothed with pale pubescence on head and prothorax, blackish on elytra, whitish and dark on under surface.

Antennae long thin and slightly infuscated. Pygidium long, apical half thin and acutely pointed. Hind tibiae with two long setose ridges, a short apical one and an inconspicuous sub-basal one, spurs very unequal, the longer one not much shorter than the following joint. Length, 3·5–4·0 mm.

PAPUA: Mount Lamington (*C. T. McNamara*).

Smaller than the preceding species, and under surface and legs red. The larger specimen has parts of the sterna and the pygidium slightly infuscated. The black setae on the tarsi are conspicuous, but as their supporting ridges diverge but slightly from the upper edge of the joints, the tarsal formula (apparently 3, 2, 2) is not well defined.

Mordellistena imponderosa, sp. n.

Black and flavous. Clothing inconspicuous, except that on some of the dark under parts it is whitish.

Antennae long and thin. Pygidium long and very thin from near the base. Length, 2·5 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Unique.

A narrow species, much smaller and decidedly thinner than the two preceding ones, and with parts of the undersurface differently coloured. The flavous parts are the head, prothorax, scutellum, apex of abdomen, pygidium, antennae, palpi, front and middle legs, hind trochanters and parts of tibiae and of tarsi. The black setose ridges of the hind legs are so little divergent from the upper edges of the tibiae and tarsi that it is difficult to be sure of their formula; there are apparently three on the tibiae (two long and one short) and apparently three on the first joint of the tarsi.

Mordellistena postcoxalis, sp. n.

Black, brilliantly iridescent, especially the head; sides of head about eyes and inner half of hind coxae pale flavous, parts of muzzle and apex of pygidium obscurely reddish. Pubescence black on upper surface, black and white on under surface and legs.

Antennae unusually long, rather stout, second to fourth joints short. Pygidium long thin and acutely pointed. Hind tibiae with two long setose ridges, a short subapical one and remnants of a sub-basal one; spurs reddish and unequal, the longer fully twice the length of the other, and almost as long as the following joint, the latter with three oblique ridges, the second and third joints each with two. Length, 4·5–5·5 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Two specimens.

A narrow black species, but very distinct owing to the colours of the head and hind coxae; the antennae are also unusually long, although smaller than in *M. megacera* from Queensland. Most of the pygidium is pale, but not as pale as part of the hind coxae. The sub-basal ridge of the hind tibiae is so inconspicuous that it might fairly be regarded as absent; but, as with so many of the species with black hind legs, the ridges are distinguishable from but few directions.

Mordellistena iridomela, sp. n.

Black, in parts brilliantly iridescent. With black pubescence, white very narrowly margining base of prothorax, on scutellum, on sides of under surface, narrow across middle of abdominal segments and on parts of legs.

Antennae long and thin, not at all serrated. Pygidium long, thin, and acutely pointed. Hind tibiae with two long oblique ridges, and a short subapical one, spurs unequal and obscurely reddish, the longer about two-thirds the length of first tarsal joint, the latter with three ridges, second with two. Length, 4 mm.

PAPUA: Mount Lamington (*C. T. McNamara*).

From the Queensland *M. atronitens* it differs in being slightly larger and more robust, pygidium somewhat stouter and less acute, and ridges of hind legs different. On one specimen the front legs are obscurely reddish. The white pubescence of the upper surface is very sparse and inconspicuous from most directions. The legs being black, it is difficult to see the setose ridges clearly.

Five other specimens from Mount Lamington probably belong to this species, but are smaller (3·0–3·2 mm.); the antennae, front legs, middle tarsi and the spurs to hind tibiae are pale, on two of them the pygidium and hind tarsi (except for the setose ridges) are also pale.

Mordellistena serratipes, sp. n.

Black, in parts iridescent, abdomen, antennae, palpi and parts of legs obscurely reddish. Pubescence blackish, in places obscurely brownish.

Antennae and pygidium long and thin. Hind tibiae with two long and two short oblique setose ridges, spurs unequal, tarsal joints with four, three and two ridges. Length, 4·2 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Unique.

Slightly less robust than the preceding species, abdomen obscurely reddish and ridges of hind tibiae different; the ridges on the tibiae and tarsi are sharply defined, and from some directions cause those parts to appear distinctly serrated.

Mordellistena bimaculicollis, sp. n.

Reddish and black or blackish, in parts iridescent. With fine pubescence, mostly pale on the reddish parts and black elsewhere.

Antennae long and thin. Pygidium long thin and acutely pointed. Hind tibiae with two long oblique black ridges and a short one, spurs flavous and very unequal, first joint of tarsus with three ridges, second with two. Length, 3·2 mm.

PAPUA: Mount Lamington (*C. T. McNamara*). Unique.

If the markings are at all constant, this should be a very distinct species. Regarding reddish as the ground-colour, the black or blackish parts are the middle of the head, a large spot on each side of the middle of the pronotum, a large spot behind the scutellum (narrowly divided by the suture), an irregular median fascia, a large apical spot (but not the extreme apex), metasternum, most of abdomen and of hind coxae and other parts of the legs.

Mordellistena dodoneae, Montr.

Specimens of this species from Samoa and New Caledonia (sent by Mr. Blair) appear to be indistinguishable from others from Mount Lamington (*C. T. McNamara*) and many taken by myself in New Caledonia (Noumea), and Fiji (Viti Levu, Taveuni, Wakaya, and Ovalau).

Mordellistena gracilicauda, Blair.

Numerous specimens from Mount Lamington agree with one sent by Mr. Blair as *M. gracilicauda* from Fiji.

FIJI.

Mordella lachrymosa, sp. n.

Black, in parts somewhat iridescent. Clothed with black and white or whitish pubescence.

Antennae rather short, fifth to tenth joints obtusely serrated. Pygidium long, thin and acutely pointed. Spurs to hind tibiae subequal, each about half the length of the basal joint of tarsi. Length, 12–13 mm.

Fiji : Moturiki, in June (*A. M. Lea*).

Structurally close to *M. leucosticta*, but with very different markings. Of the two large species tabulated by Mr. Blair from Fiji * it differs from *M. decemguttata*, Fab., in having fewer spots on the elytra and the prothoracic markings different, and from the description of *M. vitiensis*, Blair, by fewer elytral spots, base and sides of prothorax with a continuous line of white clothing, and hind coxae each with a white spot at the outer base. The clothing on the head is uniform, except that near the base (but not at the extreme base) it is more greyish than white. On the pronotum the white pubescence rather narrowly but almost evenly clothes the base, more narrowly each side, and is continued for a short distance on each side of the apex; there is also a narrow fascia across the apical third, but interrupted in the middle, from each end of the interruption a narrow vitta extends backwards half-way to the base. The scutellum has a small triangular white spot on each side of the base. On each elytron there are three distinct spots : a tear-shaped one at the basal fourth, slightly nearer suture than side, a similar one obliquely behind it, or actually touching it, and a transverse spot at the apical fourth; in addition there is some white pubescence, forming a feeble transverse spot on each side at the basal fourth, and a thin strip near the subapical spot. On the pygidium the pubescence is mostly white, but has a flea-bitten appearance. On the femora it is rather dense, and it forms conspicuous markings on the undersurface.

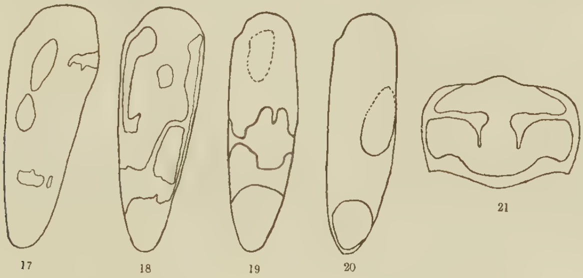

Fig. 17.—Markings of right elytron of *Mordella lachrymosa*, Lea; 18. of *Mordellistena inscripta*, Lea; 19 and 20. of *M. greenwoodi*, Blair; 21. Prothoracic markings of *Mordella lachrymosa*, Lea.

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* Blair, *Ann. Mag. Nat. Hist.*, (9), **9**: 562–3.

Four imagos and numerous larvae and pupae were taken from a fallen tree of a very light whitish wood. Compared with the figures of *Mordellistena floridensis*, in the Cambridge Natural History * the larva differs from figure A, in having no tubercular processes on the upper surface of the abdomen, and the tip more produced; and the pupa from figure B, in having shorter elytra and the pygidium more produced. The larvae bore cylindrical tunnels lengthwise in the trunk, filling them with triturated wood, as do many Longicorns, then they curve round and bore straight outwards, from about half an inch to three-quarters below the bark. Many specimens were close together in the trunk examined, and they were evidently feeding on the wood itself, and not on other insects.

Mordellistena inscripta, sp. n.

Blackish brown, under surface, antennae, palpi and legs reddish brown. Clothed with shining and rather pale (but not white) pubescence, on the elytra darker pubescence forming a pattern.

Antennae and front legs long and thin. Pygidium long and acutely pointed. Hind tibiae with five oblique black ridges, the second (from the base) slightly longer than the first, the others slightly decreasing in length, spurs unequal, the longer about half the length of the following joint, first joint of tarsi with five oblique black ridges, the basal one feeble, second with three, third with two. Length, 5 mm.

FIJI: Ovalau in June (*A. M. Lea*). Unique.

Regarding the main colour as black (although it is really dark brown), the species is readily distinguished from *M. xanthocephala* and *greenwoodi* by its larger size, very different markings and hind-legs; the other species tabulated by Blair are uniformly coloured on the upper surface. The colour and clothing are much as in *M. epicallens*, from New Guinea, the elytral pattern is also different, although evidently on the same plan; but the hind tibiae are certainly different. On the pronotum of the type there are vague indications of darker markings, but on each elytron the markings are sharply defined and consist of a narrow vitta along the basal half of the suture, each end enlarged to a spot; a jagged fascia across the apical third, meeting a narrow marginal vitta (invisible from directly above), which extends almost to the base, and giving off a narrow vitta, which extends forwards for a short distance, and is then deflected to meet the marginal one, there is also an isolated dark median spot at the basal third. The basal markings on the elytra are like a narrow X.

Mordellistena greenwoodi, Blair.

In Fiji I obtained three specimens, each about 3 mm. in length, that differ considerably from each other in markings, but are structurally so closely allied that I think they may belong to but one species, and possibly to *M. greenwoodi*, with the description of the sculpture of which they agree.

Specimen 1. Viti Levu in July.—Black, shoulders obscurely reddish, parts of antennae and of front legs still more obscurely reddish. Clothed with black and white pubescence, the latter not forming distinct patterns, except on elytra, where there are two large but ill-defined basal spots, and a distinct postmedian fascia.

Specimen 2. Taveuni in May.—Black, parts of elytra, of antennae, and of legs reddish. Clothed with black and white pubescence.

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* Sharp, *Cambr. Nat. Hist.*, VI, "Insects," 2: 268.

About half the area of the elytra is reddish, the dark parts are the suture (narrowly) a fairly large ill-defined spot on each side of the middle of the base (from some directions apparently longitudinally divided in the middle), a narrow median fascia, suddenly and strongly dilated at the middle of each elytron, and then as suddenly narrowed to the side, and the apical fourth. The pale pubescence appears to form a median vitta on the head and pronotum, but varies in appearance from every point of view, or it may even appear to be entirely absent. From all directions the pubescence on the pale parts of the elytra appears to be whitish, but from some it appears to be whitish even on the dark parts.

Specimen 3. Viti Levu.—Blackish, elytra reddish, a large ill-defined spot on the middle of each side and the apical fourth blackish, parts of under surface obscurely diluted with red, antennae, palpi and legs of a dingy reddish or testaceous. Pubescence partly whitish, but varying in appearance from every point of view.

On this specimen the black setae on the hind legs are much more conspicuous than on the others, but this is due solely to the paler colour of the surface they are upon.

Mordellistena consimilis, Blair.

Somewhat variable in length. Specimens from Taveuni, Viti Levu, Ovalau, and Mokondronga (*A. M. Lea*) agree well with a specimen from Mr. Blair.

REVISION OF THE GENUS *IOLANA*, BETHUNE-BAKER

(Lepidoptera, Lycaenidae)

By Captain A. F. Hemming, C.B.E.

[Read 5th November, 1930.]

Plate XI.

The following notes on the genus *Iolana*, Bethune-Baker, have been prepared in the light of work on the extensive material now available in the British Museum (Natural History) as the result of the accession of the Oberthür Collection. I particularly desire to acknowledge my indebtedness to the Trustees for the facilities accorded for the study of this rich material. Through Lord Rothschild's kindness, I have also been able to study the material contained in the Zoological Museum at Tring. Commander Wyndham Forbes, D.S.O., R.N., has also kindly furnished me with some interesting material from little-known localities. The dates assigned to the earlier-named forms are those given in Sherborn's *Index Animalium.* For the later ones, the best authority available in each case has been consulted. For the *camera lucida* drawings of the genitalia I am much indebted to my wife.

The genus *Iolana* was erected by Bethune-Baker (1914) for the reception of *iolas*, Ochs. (type), *gigantea*, Gr.-Gr., *coeligena*, Obth., and *astraea*, Frr. He defined it as follows :—

> " The genus has hairy eyes, the genitalia are very distinct with a broad, deeply cleft tegumen, excessively broad and large clasps, with the fore apex strongly dentate and somewhat hooked at the apex, with a long, formidable spike on the margin falling inwards. The oedoeagus is straight and broad, of moderate length, slightly and evenly tapering to the apex."

Iolana is, on the whole, nearer to *Maculinea*, Van Eecke (type *alcon*, Schiff.), than to *Glaucopsyche*, Scudd. (type *lygdamus*, Dbl.), owing to the great breadth of the clasp in relation to its length. This character is not found in *astraea*, Frr., which clearly cannot be included in *Iolana*, from the species of which it is also superficially very different. It was treated by Chapman (1913–1914) as belonging to *Glaucopsyche*, but later (1920) that author pointed out that this association was inadmissible. The nearest ally of *astraea* is *melanops*, Boisd. (1828), which Chapman (1920) also pointed out could not be assigned to *Glaucopsyche.* These species form, in fact, a group that deserves generic status fully as much as do *Glaucopsyche* and *Iolana.* For their reception, I propose the following genus.

Genus **Apelles,** gen. nov.

Similiar in general coloration to *Glaucopsyche*, Scudd.; but differs structurally from that genus in the following characters of the male genitalia :—

(i) In *Apelles,* the clasp entirely lacks the conspicuous spine which runs parallel to the distal margin of the clasp in *Glaucopsyche*;

(ii) The lower margin of the clasp in *Apelles* is curved inwards conspicuously (as though a piece had been bitten out) near the distal end; in *Glaucopsyche*, the corresponding margin of the clasp forms a straight line;
(iii) The uncus is less heavily chitinised in *Apelles* than in *Glaucopsyche*, the lobes in their ventral aspect being broader and flatter than in that genus;
(iv) The lateral apophyses of the uncus are shorter and slighter in *Apelles* than in *Glaucopsyche*.

Genotype *Apelles melanops*, Boisd. (1828) = *Polyommatus melanops*, Boisd. On the material available in the British Museum, I consider that the tribe Glaucopsychidi contains five genera, of which the most natural linear arrangement is as follows :—*Iolana*, *Apelles*, *Glaucopsyche*, *Maculinea* and *Phaedrotes*, Scudd.

Genus **Iolana,** Bethune-Baker.

Genus *Iolana,* Bethune-Baker, 1914, Ent. Rec., **26** : 162.

This genus contains only two known species, viz. *iolas* and *gigantea*. The other species cited by Bethune-Baker do not agree with his diagnosis and are referable to other genera, *coeligena* to *Maculinea* and *astraea* to *Apelles*.

1. **Iolana gigantea,** Gr.-Gr.

As will be seen from the figures given, the genitalia of this species are readily separable from those of *I. iolas*. The uncus is more massive and the lateral apophyses are broader and more swollen at the base. The clasps are almost square in shape, being nearly as broad as they are long. The distal margin forms a straight line instead of being incurved as in *iolas*, and bears only one small spine in place of the 5 or 6 seen in *iolas*. The long and massive spine falling inwards from the upper margin (which I regard as the main character of the genus *Iolana*) resembles that of *iolas*, except that on its lower margin it lacks the spur that in *iolas* protrudes towards the base of the clasp. Finally, along the upper margin of the clasp there is an irregular folded chitinous process not found in *iolas*.

This species occurs from the Alai mountains in the north-east to Gilgit in the south-west. Three subspecies have been distinguished, viz.—

(a) **Iolana gigantea gigantea,** Gr.-Gr. (Pl. XI, figs. 2, 3, 4.)

Lycaena gigantea, Gr.-Gr., 1885, Romanoff, Mém. Lep., **2** : 215, nota 4; *id., ibid.*, 1890, **4** : 418, pl. 9, figs., 8 A ♂, B ♀, "Alai, Utsch-Kurgan."

Groum's types were taken in May at an elevation of 3500 ft. In the Pamir it was found by Haberhauer in May and June. Worn specimens were taken in the beginning of June by Fedtschenko (Erschoff, 1874). This is the largest of the three subspecies of *gigantea* (Groum gives its expanse at 43–44 mm.). It is thus larger than *iolas*, Ochs., which is its nearest ally. It is, however, readily distinguishable from that species by the clear sky blue of the ground-colour of the ♂ upperside and in the ♀ by the unicolorous ground-colour, which is a warm orange brown. Besides the ♂ holotype and ♀ allotype, the British Museum now possess 3 ♂ and 3 ♀ paratypes, all from Utsch-Kurgan (Hissar Mont). All were taken in 1892, the ♂♂ from June 9th–21st, the ♀♀ from June 21st–July 2nd. These dates are probably reckoned in the Old (Russian) Style.

(b) **Iolana gigantea iphicles**, Stgr.

Lycaena iphicles, Stgr., 1886, Stett. Ent. Ztg., **47**: 227, " Alai, Oche, Samarkand (mont.)."
Lycaena gigantea var. *iphicles*, Gr.-Gr., 1890, Romanoff, Mém. Lep., **4**: 419.

Iphicles differs from nominotypical *gigantea* by its constantly smaller size. Groum gives the average expanse of his specimens as 34–36 mm. His specimens of *iphicles* were taken a little above Oche, on the banks of the Akh-Boura. In addition, *iphicles* differs from nominotypical *gigantea* as follows :—

♂ *upperside*. Ground-colour darker and greener blue (pale bright blue in type); fore-wing marginal border broader (very narrow in type).

♀ *upperside*. Ground-colour pale greyish-brown (warm orange-brown in type); no blue scales (feebly indicated in type) at base of wings except in one aberrant example from Oche, and no yellow submarginal lunules (feebly indicated in type) at anal angle of the hind-wings.

♂♀ *underside*. Black spots to submarginal lunules in Interspaces 1*c* and 2 on the hind-wings only faintly indicated (well-defined in type).

The British Museum possess two males of *iphicles*, one from Groum's coll. labelled " Mt. Hissar, *gigantea* var. *alpina* " and the other labelled " Nakuat, Fergana." The three females in the collection are all labelled " Oche, Fermana."

(c) **Iolana gigantea gilgitica**, Tytl.

Polyommatus iolas gilgitica, Tytler, Aug. 1926, J. Bombay Nat. Hist. Soc., **31**: pl. 1, fig. 16 ♂.
Polyommatus gigantea gilgitica, *id.*, 1st Nov. 1926, *ibid.*, **31**: 586, " Yasin, Gilgit."

In addition to the two males on which Tytler's description is based, Evans (1925) has recorded the capture of this subspecies at Gilgit by Colonel C. H. Hawsell, R.E. The British Museum possess one ♂ labelled " Gilgit, 5.1923," presented by Evans and presumably taken by Colonel Haswell. The Zoological Museum at Tring possess three males taken in Bashahr nearly 400 miles to the south-east of Gilgit. These specimens which agree with those from Gilgit are labelled " Prov. Bashahr, 14–16,000 ft. Spring 1912. Rev. H. B. Mara."

Gilgitica has a harder and brighter metallic blue ground-colour than the other subspecies of *gigantea*. The black marginal line is extremely narrow. From some angles the veins on the fore-wing appear lighter in colour than the rest of the wing. The ground-colour of the underside is a dirty grey without the admixture of brown seen in the other subspecies.

2. **Iolana iolas**, Ochs.

This species has by far the widest distribution of any of the known species of *Iolana*. It is known from Algeria and Spain, throughout the greater part of Southern Europe, occurring locally in scattered colonies in localities where its food-plant *Colutea arborescens* grows. In Asia Minor it is recorded from Bithynia, Pontus and the Taurus. It is found in Western Transcaspia and in North-East Persia. It is not surprising to find that a species, at once so local and so widespread, has developed a considerable number of marked subspecies.

(a) **Iolana iolas powelli**, Obth.

Lycaena iolas var. *powelli*, Oberthür, 1911, Bull. Soc. ent. Fr., **1911** (13): 268, " Géryville, dans le sud de la province d'Oran."
Lycaena iolas powelli, *id.*, 1912, Ét. Lep. Comp., **6**: 328, pl. 126, fig. 1120 ♂; *id.*, 1915, *ibid.*, **10**: 391–3, pl. 288, fig. 2340 ♀.

The British Museum now possess ♂ 13, ♀ 15 of *powelli*, including the types. All are labelled " Sudoranais, Aflou," except one pair labelled " Géryville, juin

1910 " and two females bred from larvae found at Lambèze. The most striking characters by which *powelli* can be separated from other subspecies of *iolas* are those found on the underside. On this surface, which is brownish grey in colour, the submedian spots very small and on the hind-wings often absent in two or more interspaces, the discoidal spots are very inconspicuous (*i.e.* they hardly show at all against the background); the blue scaling at the base of the hind-wings is practically absent, and the submarginal lunules are absent on the fore-wings and only slightly developed on the hind-wings. On the upperside, the black borders of the fore-wings in the ♂ are well developed, and the ground-colour is purplish blue. In the ♀, the black border to the fore-wings is narrower than in any subspecies except that from Spain. Oberthür (1922) cites the capture of *iolas* in Morocco (Grand-Atlas, Glaoui) by Vaucher, who notes that the blue ground-colour is different from that in the type.

(b) **Iolana iolas thomasi,** subsp. nov.

♂ *upperside.* Ground-colour pale bright blue without the purplish shade found in all other subspecies of *iolas*; fore-wing border relatively broad, showing tendency to form interneural spots.

♀ *upperside.* Ground-colour of the same pale bright blue as the male, black border narrow as in *iolas powelli.*

♂♀ *underside.* In general closer to, and of the same colour as, *iolas protogenes* than other subspecies, but markings differ in following particulars:—(*a*) submarginal lunules are completely absent on both fore-wings and hind-wings; (*b*) discoidal spots hardly distinguishable from ground-colour; (*c*) submedian and basal spots on hind-wings much smaller than in *protogenes,* the spot in Interspace 5 being vestigial; (*d*) the blue scaling at the base of the hind-wings greatly reduced in extent.

Length of fore-wing, 22 mm.

Habitat: Aragon, Albarracin; Nueva Castilla, Cuenca.

♂ *Holotype:* Albarracin, 18.6.1928 (*Haig-Thomas*), (B.M. Type No. Rh. 341).

♀ *Allotype:* Albarracin, 19.6.1928 (*Haig-Thomas*), (B.M. Type No. Rh. 342).

Paratypes in Hemming Coll., viz.—Albarracin, ♂, 15.6.1928 (Coll. No. 24691), ♀ 12.6.1928 (Coll. No. 24690) (*Wyndham Forbes*). Other specimens in Hemming Coll. are from Cuenca, 16.6.1928, 1 ♀ at 1200 m. and another at 1400 m. (Coll. Nos. 25125–6) (Querci).

This striking subspecies is named after Mr. P. Haig-Thomas, by whom the type specimens now in the British Museum were taken.

(c) **Iolana iolas protogenes,** Fruhst. (Pl. XI, fig. 1.)

Lycaena iolas protogenes Fruhstorfer, July 1st, 1917, Iris, **31**: 31, " Digne."

In this subspecies the marginal border to the fore-wings is, in the ♂, narrower than in *thomasi,* and the ground-colour is purplish blue ; in the ♀ the marginal border to the fore-wings is much broader. On the underside, the submedian and basal spots are well developed, and so are the submarginal lunules. In the Basses-Alpes, *protogenes* occurs locally in several places in the immediate neighbourhood of Digne. In the Bouches-du-Rhône Foulquier (1899) records it as very rare, occurring irregularly at Saint-Pons in the first fortnight of May. He adds that it formerly occurred in the neighbourhood of Aix, but has disappeared in that locality. In the Var, the same author (1923–4) records it from Nans and St. Zacharie. From the latter locality there is a fine ♂ in the British Museum taken by him in May 1909. Duponchel (1832) recorded it from Toulon and from Montvert near Saint-Maximin. Simes (1923) records the capture of a ♂ at La Sainte Baume near the Source de l'Huveaune at the end of May 1922. It is doubtful if it occurs in the Alpes Maritimes, whence it is recorded without details by Bromilow (1892) and Frionnet (1906). Rowland-Brown (1910) records the capture by Warren of two females at Nyons on June 28th, 1910, in the Department of the Drôme.

(d) **Iolana iolas wullschlegeli,** Obth.

Lycaena iolas var. *wullschlegeli*, Oberthür, 1915, Ét. Lep. Comp., **10**: 392, pl. 288, fig. 2341 ♀, "Follaterre près Martigny, Valais."
Lycaena iolas eurysthenes, Fruhstorfer, July 1917, Iris, **31**: 31, "Wallis, Follaterres."

In this subspecies, the ground-colour on the upperside is deep purplish-blue, and in the females the blue area is much smaller than in any of the other species owing to the extension of the brownish-black border. On the underside the ground-colour is a darker ash-grey than in *protogenes*, the discoidal spots are clearly outlined black and the submedian spots and the submarginal lunules are more strongly developed.

Wullschlegeli appears to be confined to the Canton Valais in Switzerland, occurring at Sierre, Sion and elsewhere as well as in the neighbourhood of Martigny. Vorbrodt (1912) records *iolas* from the Tessin and refers to especially large examples taken at Misox. In the absence of material, it is not possible to say whether the Tessin *iolas* are referable to *wullschlegeli* or to some other subspecies.

(e) **Iolana iolas iolas,** Ochs.

Lycaena iolas, Ochs., 1816, Schmett. Europa, **4**: 144, "Ungarn."

Nominotypical *iolas* is in some respects intermediate between *protogenes* and *wullschlegeli*. The black marginal border on the upperside of the fore-wing of the female is narrower than in the latter, but much wider than in the former. On the underside the ground-colour is paler and less cold in tone that in either of those subspecies and the submedian spots are considerably smaller. The submarginal lunules are fairly well developed both on the fore-wings and on the hind-wings.

The British Museum possess ♂ 14, ♀ 15 from Hungary and 1 ♀ from the Banat. Verity and Querci (1923) record this subspecies from Santuario della Civita, 800 m., and in the Province of Caserta and from Fonte Tempesta, near Genzano (Rome). The only Italian specimen in the British Museum is labelled "It. merid., Avellino et Paternopoli. 7.1907 *Fabresse*." Commander Wyndham Forbes took this species at Pozzuoli near Naples in June 1912; and saw, but failed to catch, it at Taormina in Sicily. On the Dalmatian coast the same collector has obtained this species between Ragusa and Ragusa vecchia. Mrs. Nicholl (1899) observed it in 1898 at Blagaj 8 m. E. of Mostar (11.vi.), at Travnik (22.vi.), and on the lower slopes of the Baba Planina, 16 m. S.E. of Gacko (11.vii.).

(f) **Iolana iolas bureschi,** subsp. nov.

♀ *upperside*. Uniform blackish brown, faintly scaled with blue at the base of the wings.

♀ *underside*. Ground-colour ash grey of a much browner shade than in *iolas iolas*, being nearer to that of *iolas wullschlegeli*; submedian spots and submarginal lunules larger and more sharply defined than in *iolas iolas*.

Length of fore-wing, 22 mm.

Habitat: Bulgaria, Slivno.

♀ *Holotype:* "S.W. Bulgaria, Slivno, 1899, Nicholl"; B.M. Type No. Rh. 347.

This subspecies which is named in honour of Dr. I. Buresch, the Curator of the Royal Museum, Sofia, seems to be extremely local in Bulgaria, not being found apparently except in the immediate neighbourhood of Slivno (Rebel, 1903). Mrs. Nicholl (1900) found it "very common" in this locality on May 23rd, 1899, and on May 31st she also took it in the gorges of Tschatalka. It is the largest and darkest subspecies of *iolas* known.

(g) **Iolana iolas andreasi,** Shelj.

Lycaena iolas andreasi, Sheljuzhko, Dec. 1919, N. Beitr. syst. InsektK., **1**: 129, "Transcaspien:—Firuza bei Askahabad."

In this much smaller subspecies the ground-colour is a dark violet-blue and the marginal border in the male is wider than in *iolas iolas*. In the female the black border is so greatly enlarged that the upperside is substantially blackish-brown with only a purplish-blue suffusion at the base of the wings. The ground-colour of the underside is pale ash-grey without the brownish tone seen in *iolas bureschi*. The submedian spots of the fore-wings are well-developed, but those of the hind-wings are small. The submarginal lunules of the fore-wings are almost obsolete. The blue scaling at the base of the hind-wings is more extensive than in *iolas iolas*.

The British Museum possess ♂ 2, ♀ 1, taken at Kedos (Western Asia Minor), 21–24.5.1918, by Major N. V. L. Rybot, D.S.O. In the Zoological Museum, Tring, there is a third ♂ of this series taken on May 28th. The British Museum possess a ♂ labelled "Tokat, 1906." There is a ♀ of this subspecies at Tring labelled "Taurus," in which there is very little blue scaling at the base of the wings, and a ♂ labelled "Budshnurd, Upper Atrek River, North Persia, August 1903."

Genus **Maculinea,** Van Eecke.

This genus, of which *M. alcon*, Schiff. (1775), is the type, contains six or seven species of which the most widely distributed is *M. arion*, L. (1758). It is proposed here to discuss only *M. coeligena*, which was included by Bethune-Baker in *Iolana*, and the closely allied and little-known species *M. coelestis*.

1. **Maculinea coeligena,** Oberth.

This species, which is purely oriental, occurs in two well-marked subspecies, one of which is undescribed.

Superficially it differs very strikingly from all the known species of *Maculinea* (except *M. coelestis* described below) by the intense metallic blue ground-colour of the upperside of the wings in the males. The genitalia, especially as regards the form of the uncus and its lateral processes, are, however, very similar to those found in other species of *Maculinea*, from which they may be distinguished by the following characters:—

(*a*) the clasps are relatively very short and broad instead of being much longer than they are broad as in all the other species except *M. coelestis* (for which see below),

(*b*) the upper and lower margins of the clasps in the other species are more or less parallel to one another, but in this species the clasps are much wider at their distal end than at the base, (*c*) the distal margin of the clasp is irregularly incurved and the terminal spine is broader at the base and more rounded and tapering than in the other species of *Maculinea.*

(a) **Maculinea coeligena coeligena,** Oberth. (Pl. XI, fig. 5.)

Lycaena coeligena, Oberthür, 1876, Ét. d'Ent., **2**: 21, pl. 1, figs. 3A, B ♂, "Moupin."

The British Museum now possess Oberthür's type, which is labelled "Chine, Moupin, *R. P. Armand David.*" In addition the collection contains ♂ 11, ♀ 6; some are from Ta-Tsien-loù taken in 1893 and 1897; the remainder are labelled "Frontière orientale de Thibet—*Chasseurs de Dejean,* 1905." All the above specimens were received with the Oberthür Collection. They are strikingly different from Leech's Hupeh *coeligena* described below, which previously were the only specimens of this species possessed by the Museum.

(b) **Maculinea coeligena pratti,** subsp. nov.

Lycaena coeligena, Oberthür, Leech *nec* Oberthür, 1893, Butt. China, (2): 312.

Differs from *coeligena coeligena* as follows:—

♂ *upperside.* Black border to the fore-wing and narrower, and the black apical patch smaller; ground-colour brighter metallic blue, the whitish reflection much less marked.

♀ *upperside.* Blue scaling much more brilliant and metallic and with no whitish tinge; the veins much less definitely outlined with darker scales.

♂ *underside.* Basal and discal area of the fore-wing unicolorous palish brown instead of pale whitish grey with the veins outlined in brown. Hind-wings similar to those of type subspecies.

♀ *underside.* Basal and discal area of the fore-wing unicolorous and of a warm brown colour instead of a palish brown, with whitish patches between the end of the discoidal cell and the submedian spots and with the veins outlined in brown.

Average length of fore-wing, 20 mm. (21 mm. in type).

Habitat: Hupeh, Ichang and Chang-Yang, 6000 ft.

♂ *Holotype:* "Chang-Yang, 6000, *Native Collectors,* 1889" (B.M. Type No. Rh. 343).

♀ *Allotype:* "Chang-Yang, May 1888, *A. E. Pratt*" (B.M. Type No. Rh. 344).

Paratypes (♂ 5, ♀ 7) from the above localities in the British Museum. The whole of the above material formed part of the Leech Collection.

2. **Maculinea coelestis,** Alpheraky.

This fine species was entirely unrepresented in the British Museum until the accession of the Oberthür Collection, which contained ♂ 34, ♀ 17 of the nominotypical subspecies and ♂ 4, ♀ 3 of an undescribed subspecies from Tsékou (Tseku).

The genitalia differ from those of the other species of *Maculinea* in the same way as do those of *M. coeligena,* from which it may be separated by the form of the clasps, the upper and lower margins of which are substantially parallel to one another instead of running towards one another basally as in *coeligena.* The terminal spine is thicker and more irregular in outline and tapers more towards the tip than in *coeligena* or other species.

(a) **Iolana coelestis coelestis**,* Alph. (Pl. XI, figs. 6, 7.)

Lycaena coeligena var. (?) *coelestis*, Alph., 1897, Romanoff, Mém. Lep., **9** : 113, "Kham."
Lycaena coeli, Oberthür, Oct. 1908, Ann. Soc. ent. Fr., 77 : 311, pl. 5, figs. 1 ♂, 2 ♀, "Rencontrée a 6–8 journées de marche au nord-ouest de Ta-Tsien-Loù."

One ♂ of *coelestis* was taken in the Province of Kham on May 20th, 1893, in the neighbourhood, and presumably to the west, of Batang by Kachkarow, the assistant who that year accompanied the celebrated explorer G. N. Potanine. Alpheraky compares this specimen with *coeligena* from Ichang (i.e. *coeligena pratti*) as follows :—" . . . diffère de nos individus d'Ichang, par une teinte bleu plus brillante, par l'apex des supérieures plus étroitement noir et par les points noirs des supérieures, sur le dessous bien plus grands, plus oblongs et plus nettement cerclés de blanc." These are also exactly the characters by which Oberthür's *coeli* differs from *coeligena*, and there is no doubt that *coeli* is a synonym of *coelestis*.

The labels on Oberthür's specimens, now in the British Museum, are as follows :—

" Ta-Tsien-Loù, 1895."
" Moenia, mai-juin 1893."
" Frontière orientale de Thibet—*Chasseurs indigènes de Dejean*, 1905."
" Moupin."
" Ta-pin-tze. *R. P. Delavay*."

It will be seen, therefore, that *M. coelestis* occurs over a large region in company with *M. coeligena*.

(b) **Maculinea coelestis dubernardi**, subsp. nov.

Much smaller than *coelestis coelestis* from which it also differs in the following respects :—

♂ *upperside*. Ground-colour deep purplish-blue instead of a brilliant metallic blue.

♀ *upperside*. Dark brown with much less blue scaling, that which is present being of the same purplish colour as the ♂ instead of a brilliant metallic blue.

♂♀ *underside* :—*Fore-wings*. No submedian spot in interspaces 1 and 5 (present in type subsp.), the spots in interspaces 2 and 3 much smaller, and that in interspace 4 very small (well defined in type subsp.), submarginal chevrons vestigial (well defined in type subsp.). *Hind-wings*. Ground-colour reddish-brown instead of greyish-brown; submedian spots and submarginal chevrons still less clearly defined against background (rather indistinct in type subsp.).

Average length of fore-wing, ♂♀ 19 mm. (22 mm. in type subsp.).

Habitat : Tsékou.

Described from ♂ 4, ♀ 3 formerly in the Oberthür Collection, now in the British Museum, labelled " Tsékou, *P. Dubernard*, 1898."

B.M.Types No. Rh. 345 ♂ holotype; 346 ♀ allotype, labelled as above.

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* Oberthür was, no doubt, unaware of Alpheraky's *Lycaena coelestis* when he described (1908, Bull. Soc. ent. Fr., **1908** : 23) as *Lycaena bellargus*, Rott., var. *coelestis*, the very distinct subspecies found in the west of France (Vendée, the two Charentes and the Bordelais). As Oberthür's name is a primary homonym of Alpheraky's and therefore invalid (Article 36 of the International Code), it is here replaced by **pictonensis**, nom. nov., in allusion to the *Pictones* or *Pictavi* by whom what is now the Vendée was formerly inhabited. This subspecies should therefore be known as *Uranops bellargus pictonensis*.

Genus **Apelles,** Hemming.

1. **Apelles melanops,** Boisd.

This species was not included by Bethune-Baker in *Iolana*, with the revision of which this paper is concerned. The following brief reference to it is, however, included here, in order to complete the description of the species of *Apelles*. Four subspecies have been distinguished.

(a) **Apelles melanops melanops,** Boisd.

Polyommatus melanops, Boisd., (1828), Europ. Lepid. Index : 13 " *Galloprov., circa* Aix."
Lycaena melanops, Freyer, 1829, Beitr. Gesch. europ. Schmett., **3**, (17) : 5 pl. 97, figs. 1 ♂, 2 ♀, " Aix, in der Provence."
Papilio saportae, Geyer in Hübner, [1827–32] Samml. europ. Schmett. **i** (no text), pl. 188, figs. 922–3 ♂, 924–5 ♀.

This species was discovered near Aix by the Count de Saporta, after whom it was named by Geyer in ignorance that it had already been named *melanops* by Boisduval. It was also given the latter name independently by Freyer. This Mediterranean species occurs over a fairly wide area in the south of France, being recorded from the following ten Departments :—Alpes-Maritimes, Var, Bouches-du-Rhône, Basses-Alpes, Hautes-Alpes, Vaucluse, Gard, Ardèche, Haute-Garonne and Pyrénées-Orientales.

In addition, there are in the British Museum ♂ 2, ♀ 2 ex Gr.-Gr., and Elwes Colls. Labelled " Corse."

(b) **Apelles melanops marchandii,** Boisd.

Argus marchandii, Boisd., 1836, Rev. Ent., **2** (3) : 121, pl. 27, " Environs de Barcelone."
Scolitantides melanops race *diversa*, Sagarra, 1926, Butll. Inst. catal. Hist. nat., (2) **6** : 136, " Barcelona, Llinas."

Boisduval's type is now in the British Museum (ex Oberthür Coll.). It was taken by Cantenet on May 10th, 1833, in the pine-woods on Mont Serrat near Barcelona. This name has usually been applied by later writers to aberrant specimens from any locality in which the spotting of the underside is obsolete. As, however, the Catalonian subspecies is characterised, in addition to its smaller size, precisely by the reduction of the underside spotting on the hind-wings, there is no justification for ignoring the name proposed by Boisduval, although his type shows these characters in an exaggerated (aberrant) degree. The ground-colour of the underside of this subspecies is browner, and less grey than that of the other known subspecies of *melanops*.

(c) **Apelles melanops williamsi**, subsp. nov. (Pl. XI, fig. 8, 9.)

Differs from *melanops melanops* as follows :—

♂ *upperside.* Ground-colour a darker purplish tone of blue, black marginal border (fore-wings and hind-wings) conspicuously broader, especially at apex of fore-wing; on the fore-wings (and in several specimens on the hind-wings) there is a series of black interneural submarginal spots partly embedded in the black marginal border.

♀ *upperside.* In general similar to *melanops melanops*, being blackish-brown scaled with blue at the base of all four wings; but differs from that in the dark purplish shade of the blue scaling.

♂♀ *underside.* Ground-colour much paler, being pale whitish-grey, as compared with the cold grey (sometimes darkish grey) of *melanops melanops*; the black submarginal spots smaller than in *melanops melanops*; hind-wings often with conspicuous whitish marginal chevrons.

Average length of fore-wings, 15–16 mm. (12–13 mm. in *melanops melanops*).

Habitat: Coastal Regions of Portugal, Oporto (type) and North-West Spain, Pontevedra.

♂ *Holotype:* Portugal, Oporto, 22.4.1914 (*R.S. Gwatkin-Williams*) (Hemming Coll. No. 9716).

♀ *Allotype:* Portugal, Oporto, 1.5.1914 (*R.S. Gwatkin-Williams*) (Hemming Coll. No. 9724).

Paratypes: ♂ 8, ♀ 5 taken at Oporto (at the same time as the type) in Hemming Coll. (Coll. Nos. 9717–9723, 9725–9730); of these, a pair has been added to the British Museum Coll. (B.M. Types No. Rh. 359 ♂, 360 ♀); ♀ 1 N.W. Spain, Pontevedra (ex Chapman Coll.) (Coll. No. 9731).

This subspecies is named in honour of Commander Gwatkin-Williams, R.N., by whom the typical series was taken. It is a very distinct subspecies, its pale lightly-spotted underside being very different from that of any other subspecies of *melanops*. It affords an interesting parallel with *Philotes baton occidentalis*, Hemming (1929), which, also confined to Portugal, differs greatly from the other Iberian subspecies of *baton* and is much nearer in general appearance to the subspecies of Southern France.

(d) **Apelles melanops algirica,** Heyne.

Lycaena melanops var. *algirica*, Heyne, in Ruhl, 1895, Pal. Grossschmett, **1** : 768, " Algerien :—Nemours, Algier, Maeta und Lambessa."

Lycaena melanops var. *algirica*, Heyne-Ruhl, Oberthür, 1910, Ét. Lep. Comp., **4** : 319; *id.*, 1915, *ibid.*, **10** : 390 pl. 290, figs. 2359 ♂, 2360–2362 ♀, " Algérie, Lambèse et Sebdou."

This subspecies is characterised in both sexes by its larger size, by the darker tone of the ground-colour on the underside and by the great increase in size of the black submarginal spots of the fore-wings on the underside. In the male, the black marginal border is considerably broader than in *A. m. melanops*. The females are frequently marked with a series of bluish-white crescents along the margins of the wings on the upperside.

This subspecies appears to be fairly widely distributed in Algeria, where it is the only subspecies known. It occurs also in Southern Spain, *e.g.* in Prov. Malaga at Malaga (Oberthür Coll.), in Prov. Almeria at Tijola (Oberthür Coll.), in Andalusia, Granada, 15.4.1927 (*C. van Straubenzee*), and in Murcia, Sierra Espuña, 24.4.1927 (*C. van Straubenzee*) (specimens from the last two named localities in Hemming Coll.). It occurs also in parts of the mountainous region of Central Portugal, *e.g.* in the Serra da Estrela, where Querci took a few specimens in July 1927.

(e) **Apelles melanops alluaudi,** Oberthür.

Lycaena melanops var. *alluaudi*, Oberth. 1922, Ét. Lep. Comp., **19** (1) : 113, " Grand-Atlas; Glaoui (*Vaucher*). Haute-Reraya, entre Asni et Arround (1,600 à 2,000 mètres) (*Ch. Alluaud*)."

This Moroccan subspecies was named by Oberthür after M. Alluaud, by whom the types were taken at Haute-Reraya. It resembles *algirica* in its large size and in the greater width (in relation to other subspecies) of the black marginal border on the upperside in the males. On the underside it is characterised by the dark grey ground-colour. The females on the upperside differ from *algirica* by their uniformly black colour. They have no traces of the blue scaling which is characteristic of that subspecies.

2. **Apelles astraea,** Freyer. (Pl. XI, fig. 10.)

Lycaena astraea, Frr., 1851, N. Beitr., **6** : 161, pl. 583, fig. 1 ♂, 2 ♀, "Amasia."

This species, which appears to be local, varies very little. Freyer's type came from Amasia, but Staudinger failed to find it in that locality. Kindermann found it in the higher mountains around Tokat, where it was by no means uncommon. Rebel records (1917) its capture by Tolg in the Amanus Mountains at Yarbashi (Jarbaschi). The British Museum possess specimens from Amasia (♂ 3, ♀ 3), Tokat (♂♀), Malatia (♂ 4) and Mesopotamia (♂ 3). There is a ♂ in the Hemming Coll. from Konia (Anatolia) and another (ex Oberthür Coll.) in the British Museum. The specimens from Malatia are a greyer and less purplish blue than those from the other localities, but this may be due to defective condition.

The genitalia of this species are in general very similar to those of *A. melanops*, from which they are, however, easily separable (*a*) by the much larger and deeper indentation at the distal end of the lower margin of the clasp, (*b*) by the outline of the upper margin of the clasp, which is straight (instead of being incurved), and (*c*) by the presence of a chitinous process lying parallel to the upper margin of the clasp (which may perhaps be regarded as a vestigial spine of the type seen in the genus *Iolana*).

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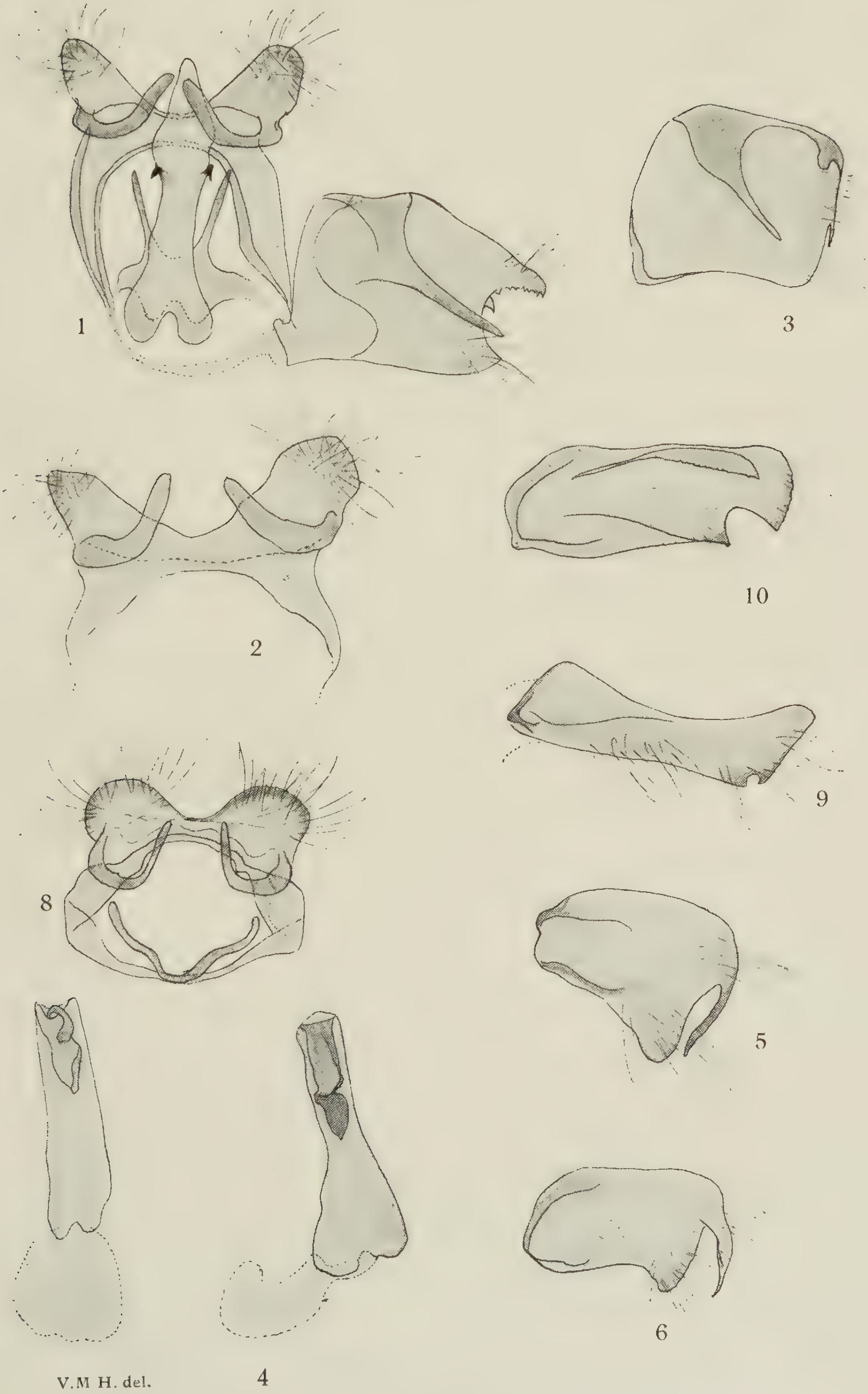
Explanation of Plate XI.

Genitalia of *Iolana*, *Maculinea* and *Apelles*.

Fig. 1. *I. iolas protogenes*, Fruhst. Basses-Alpes, Digne.
2–4. *I. gigantea gigantea*, Gr.-Gr. Hissar Mont, 21.6.1892 (paratype).
5. *M. coeligena coeligena*, Oberth. Frontière orientale de Thibet.
6–7. *M. coelestis coelestis*, Alph. Thibet, Chasseurs de Ta-tsien-Lou (paratype of *coeli*, Oberth.).
8–9. *A. melanops williamsi*, Hem. Portugal, Oporto, 1.5.1914 (paratype).
10. *A. astraea*, Frr. Anatolia, Konia.

Note.—All the specimens figured are drawn by *camera lucida* to a uniform scale. Fig. 1 shows the ventral aspect of the genitalia with aedoeagus and one clasp. Figs. 2 and 8 show the ventral aspect with the aedoeagus removed. Figs. 3, 5, 6, 9, 10 are drawings of individual clasps. Figs. 4 and 7 are drawings of the aedoeagus.

All the specimens from which the preparations illustrated have been made are in the Hemming Collection, except Nos. 2–5, which are in the British Museum.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Genitalia of *Iolana*, *Maculinea* and *Apelles*

A NEW SPECIES OF *FORCIPOMYIA* (DIPTERA, CERATOPOGONIDAE) FROM THE TRANSVAAL, WITH A DESCRIPTION OF ITS EARLY STAGES

By Botha De Meillon, M.Sc.

(South African Institute for Medical Research, Johannesburg, South Africa).

[Read 4th March, 1931.]

With Seventeen Text-figures.

Forcipomyia randensis, sp. nov.

The larvae of this midge were found beneath the bark of a dead pine stump. They were seen to be feeding on the rotting bark and cambium, and together with the pupae were present in fairly large numbers.

The Adult.

A small black species with conspicuous yellow banding on the legs and with the wings adorned with pale spots. This latter characteristic places it close to *F. chrysolopha*, K., *F. squamipennis*, Ing. & Macfie, *F. lepidota*, I. & M., *F. venusta*, I. & M., and *F. pampoikila*, I. & M. It differs from *F. chrysolopha* in the nature of the male and female antennae and from the others chiefly in the structure of the male hypopygium, *e.g.* the greatly expanded apex of the clasper and the nature of the aedoeagus.

Wing length, female, 1·2 mm.
,, ,, male, 1·5 mm.

Female.

Head : antennae (Fig. 1) with the second segment black; segments three to ten pear-shaped, dark, with paler hairs, each segment bears two colourless spines; segments eleven to fifteen more elongate, more or less of equal length and bearing fine scattered hairs; apical segment about three times as long as wide at the base with a small terminal style. Palps very dark, the third segment swollen and bearing a sensory pit (Fig. 2). Clypeus very dark. *Thorax :* mesonotum black with narrow curved, short, golden scales and longer yellowish and black bristles; scutellum black with narrow curved yellowish scales. Pleurae dark. Axillary chord pale. Halteres with pale crowns. *Wings* (Fig. 3): first radial cell obliterated, second small; costa with distinct narrow scales broader than those on the wing surface; wing adorned with pale patches as follows :—a prominent yellowish area at

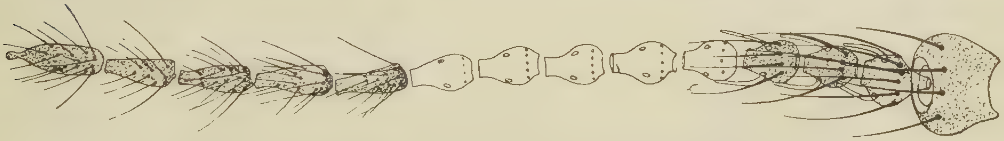

Fig. 1.—*Forcipomyia randensis*, sp. nov., female antenna, hairs and spines removed from segments 6–10. × about 88.

the end of the costa, a pale patch on the stem, or at the fork of the median and one on the stem of the cubitus; one on the base of the radius and pale areas along the border of the wing at the apices of the marginal cells. *Legs :* the relative lengths of the first, second and third tarsi are as follows :—

	1st tarsus.	2nd tarsus.	3rd tarsus.
Hind-leg . . .	8	10	7
Mid-leg . . .	8	9	5
Fore-leg . . .	8·5	6	4

Fore-leg, femur black with a small yellowish spot at the apex and a yellowish band about the middle; tibia black with pale base and apex and a yellowish band about the middle; first tarsus with apex pale; rest of the tarsi brown with paler apices except the last which is all brown. Hind-leg, femur all black, or yellowish band near the middle only slightly indicated; tibia with a small pale spot at the base, a broader yellowish band at the apex and a pale band near the middle; all, tarsi black or dark brown with pale apices except the last which is all brown; apex of the tibia with a row of closely set spines. *Abdomen :* black with long dark bristles; spermathecae more or less globular, small length of the duct chitinised.

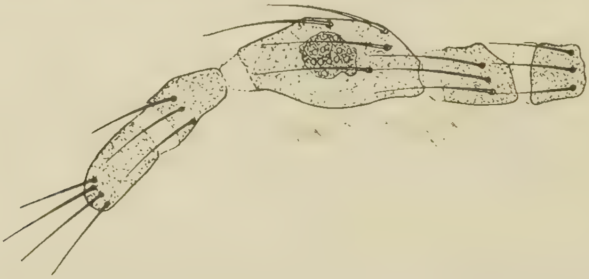

Fig. 2.—*Forcipomyia randensis*, sp. nov., female palp. × 300.

Male.

Head : antennae (Fig. 4) with long whorls of black bristles, on segments three to eleven, these bristles are paler at their apices; segments twelve to fifteen are elongate, segment fifteen is about equal in length to fourteen, the latter is three-quarters of thirteen, which is a little more than half as long as segment twelve. *Wings :* pale areas more extended than in the female; the wing is also longer and narrower. *Abdomen :* scaling not so dark as in the female, bristles longer and more numerous. *Legs :* long, bristles more numerous than in the female; proportions of the tarsi approximately as in the female. *Hypopygium* (Figs. 5 and 6) : not inverted; posterior prolongation of the ninth tergite with two lateral

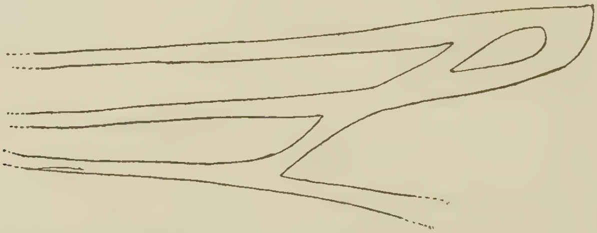

Fig. 3.—*Forcipomyia randensis*, sp. nov., radial cell and end of costa of female wing. × about 88.

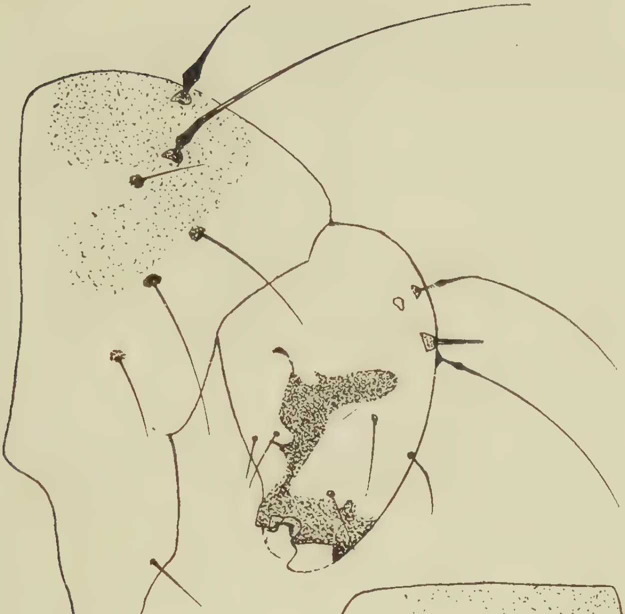

Fig. 7.

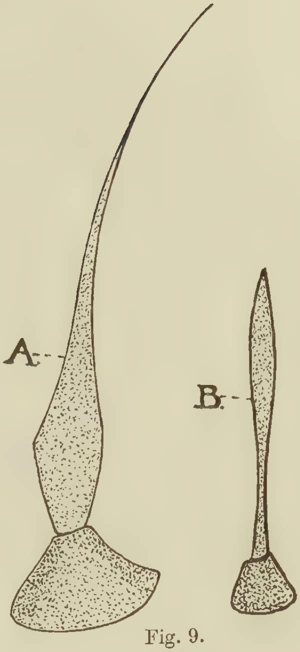

Fig. 9.

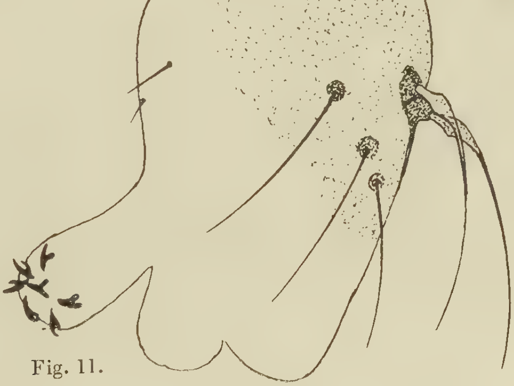

Fig. 11.

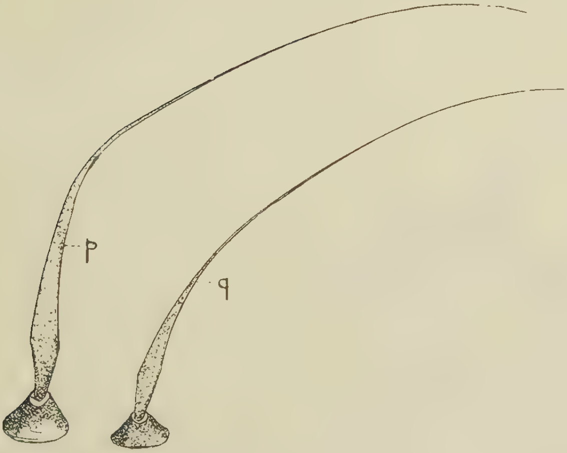

Fig. 8.

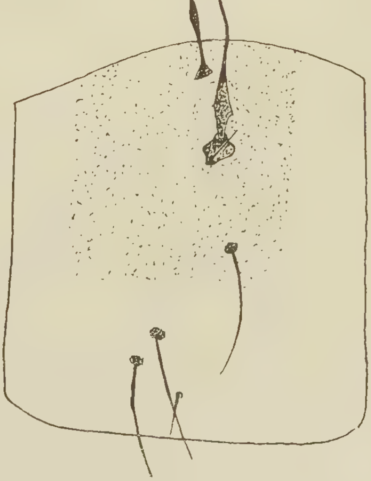

Fig. 10.

Forcipomyia randensis, sp. nov. Fig. 7, head and first thoracic segment of the larva, × 104; 8, setae "p" and "q," × 300; 9, setae "a," × 450; A = first thoracic. B = second thoracic; 10, first abdominal segment, × 104; 11, posterior half of the eighth abdominal segment, × 150.

subapical hairs, lateral processes with four delicate hairs each; this tergite is produced posteriorly in the middle line where it is very weakly chitinised; the side pieces are oval in shape and bear long bristles; claspers expanded apically and shorter than the side pieces; the parameres are simple chitinous rods articulating basally with an internal projection of the side pieces, they reach beyond the apex of the aedoeagus; the aedoeagus is complicated, poorly chitinised basally but heavily chitinised apically; it apparently consists of two parts connected by a delicate membrane; the character of the aedoeagus is best appreciated by referring to the figures, especially the lateral view (Fig. 6) in which the double nature of the aedoeagus is best seen.

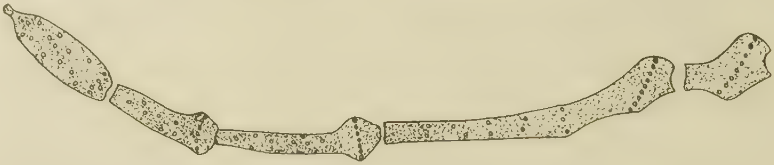

Fig. 4.—*Forcipomyia randensis*, sp. nov., terminal segments of the male antenna. × 300.

The Larva.

The nomenclature of the setae adopted here is that proposed by Saunders (1).

Length, 3·7–3·9 mm.

The larvae are dull white or cream coloured except for the head which is brown and the dark intestine, when it contains food. They are very conspicuous objects on the dark brown surface of the pine trunk on which they browse.

Head (Fig. 7): brownish and unadorned; the black hypopharynx and mouth structures easily visible; antennae short and straight; the sensory hairs *p* and *q* (Fig. 8) long and tapering to a delicate point, swollen, a very short distance from the base; other setae simple and distributed as in the figure.

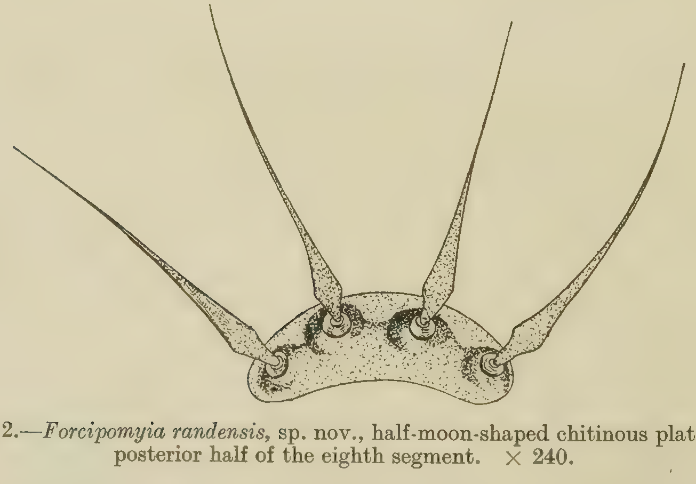

Fig. 12.—*Forcipomyia randensis*, sp. nov., half-moon-shaped chitinous plate of the posterior half of the eighth segment. × 240.

Body : setae *b* and *d* (Fig. 7) arise from a common tubercle except on the first thoracic segment where they are separate, and on the anterior half of the eighth abdominal segment where *d* is wanting; seta *b* is long, tapering to a delicate point and swollen near the base on

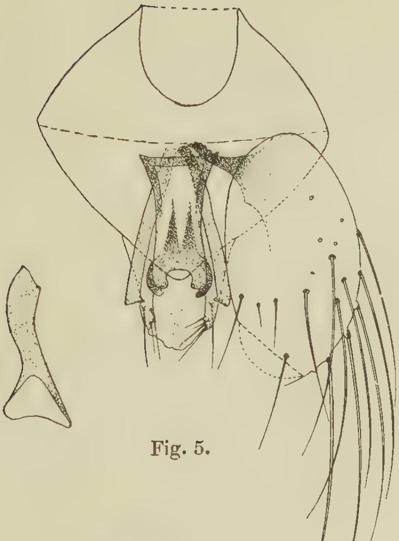

Fig. 5.

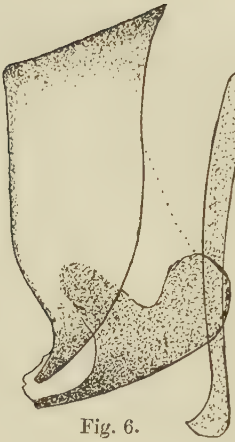

Fig. 6.

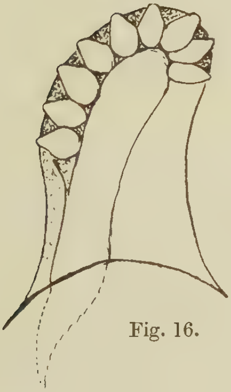

Fig. 16.

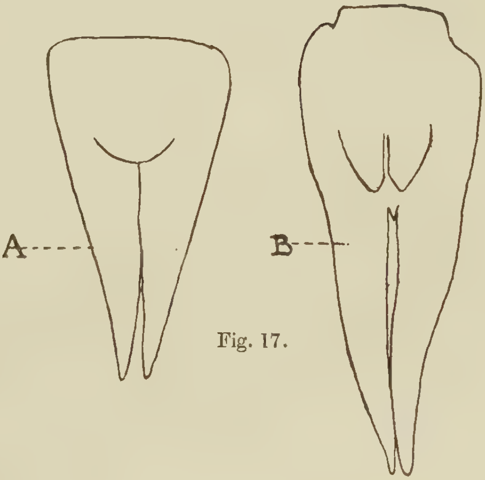

Fig. 17.

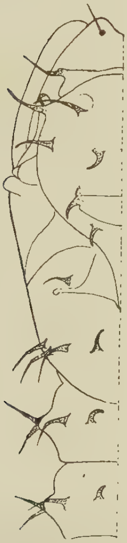

Fig. 15.

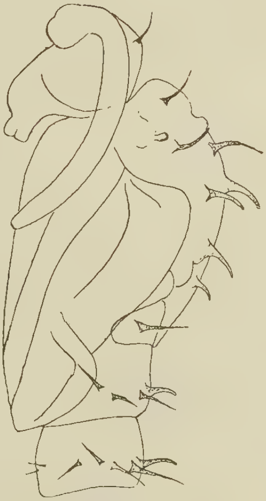

Fig. 14.

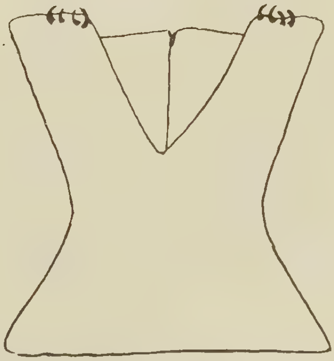

Fig. 13.

Forcipomyia randensis, sp. nov. Fig. 5, male hypopygium ventral view, × 225 ; 6, the same, side view × 450 ; 13, prothoracic pseudopod of the larva, × 150 ; 14, side view of the cephalothorax and three abdominal segments of the pupa, × about 50 ; 15, dorsal view of the same, × about 50 ; 16, trumpet of the pupa, × 700 ; 17, posterior extremity of pupa, × 104. A = female. B = male.

all segments; seta *d* is much smaller and simple; seta *a* (Fig. 9) on the first thoracic segment tapers to a delicate point, is smaller than seta *b*, but more swollen near the base; on the other thoracic segments and all abdominal segments it is much smaller and lanceolate (Fig. 9); a thin cuticular bar connects the setae of all abdominal segments. In the larvae examined by Saunders this bar is absent from the first abdominal segment. The setae *e*, *f* and *c* are all simple and mounted on small tubercles (Fig. 10); the posterior half of segment eight (Fig. 11) has its setae arranged quite differently from that of the other segments, there are four setae, similar to seta *a* of the first thoracic segment but larger, mounted on a common halfmoon-shaped chitinous base (Fig. 12); behind these four setae is a semicircular row of six simple setae mounted on separate tubercles. The ventral microchaetae are arranged as follows:—one pair before the base of the prothoracic pseudopod; meso- and meta-thorax with one pair each; abdominal segments one to eight with two pairs each gradually increasing in size from before backwards; posterior half of segment eight also bears two pairs, but they are placed closer together and are smaller. The larvae examined by Saunders bore five pairs of ventral microchaetae on the posterior half of the eighth abdominal segment.

Prothoracic pseudopod (Fig. 13): cleft in the middle and bearing the usual spines.

Posterior pseudopod (Fig. 11): very well developed, apparently more so than in the larvae examined by Saunders, for he refers to it as a fleshy ring bearing hooks. In the present larva it is cleft in the middle each branch bearing 5–6 hooks apically and 3–4 on the inner lateral side.

Malpighian tubules: three in number.

THE PUPA.

The pupae are dull white until just before pupation, when they become darker. The larval pelt is usually attached to the last three abdominal segments and is firmly fixed to the surface of the stump. The larvae being gregarious, the pupae are usually found close together.

Cephalothorax (Figs. 14 & 15): the anterior or cephalic portion bears a pair of papillae with a terminal spine each; dorsally the thoracic portion bears seven pairs of papillae, two pairs of which bear terminal spines. The trumpets are very small (Fig. 16) and not expanded apically or only very slightly so, the tracheal trunk gives off 9–10 branches as in the figure. *Abdomen:* one pair of dorso-lateral papillae with terminal spines on all segments except the eighth, where they are rudimentary and represented by a pair of small tubercles; one pair of dorsal papillae, without terminal spines, on all segments except the first and the last; three pairs of lateral papillae armed with terminal spines on segments three to eight gradually increasing in size from before backwards; on segment two there are only two lateral papillae and on segment one there are none; there are two pairs of small papillae with terminal spines on the ventral surface of segments three to eight decreasing in size from before backwards. The last abdominal segment bears a pair of long tapering processes; about as long as the last three segments in the male (Fig. 17) and the last two in the female.

Parktown North, Johannesburg, Transvaal. Larvae and pupae from a dead pine stump (Coll. *Zoë le Roux*). A few males on a room window, February, 1930.

Type, in the British Museum. Co-types in the museum of the South African Institute for Medical Research, Johannesburg, South Africa.

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NEW AFRICAN LYMANTRIIDAE IN THE BRITISH MUSEUM COLLECTION

By C. L. Collenette.

[Read 4th March, 1931.]

Plates XII and XIII.

In the following paper Ridgway's *Color Standards and Color Nomenclature*, 1912, has been employed in the colour descriptions, and the Comstock-Needham system for the wing-neuration. I have used the term patagium to indicate the collar tippet, and tegula for the wing-base cover.

All types, unless otherwise stated, are in the British Museum collection.

I am indebted to Mr. W. H. T. Tams for kind assistance rendered during the writing of the descriptions.

Stilpnotia platyrhabda, sp. nov.

(Plate XII, fig. 13.)

♂. Palpus orange buff, on the upperside fuscous. Antennal shaft whitish, pectinations drab. Frons orange buff, grading towards the vertex to cartridge buff; remainder of head cartridge buff. Thorax and abdomen cartridge buff to whitish. Fore-leg whitish, on the inner side fuscous, the tarsus entirely fuscous save for a whitish stripe down the outer side; middle leg whitish, the lower half of tibia and the entire tarsus fuscous in front; hind-leg entirely whitish. Pectus and venter cartridge buff to whitish. Fore- and hind-wing whitish, the latter of a rather more pure white than the former; on the discocellulars of the fore-wing a fuscous stripe about half a millemetre broad; fringes whitish. Underside of both wings, and fringes, whitish; proximal half of costa of fore-wing lightly shaded with fuscous.

♀. Resembles the ♂, but without the fuscous shading on the costa on the underside of fore-wing.

Expanse: ♂♂ 22–24 mm., ♀♀ 31–34 mm.

1 ♂ (holotype), 1 ♀ (allotype) and 9 ♂♂ (paratypes) wet season, October–November 1912 and 1913; 1 ♂ (paratype) dry season, 6.vii.1909, and 2 ♀♀ (paratypes) dry season; all Bitje, Ja River, Cameroons, 2000 ft., *G. L. Bates* (ex Joicey collection); 1 ♂ (paratype) Johann-Albrechts Höhe, Cameroons, 1896, *L. Conradt*, (ex Oberthür collection); 1 ♀ (paratype) Cameroons, November, *G. Schwab* (ex Joicey collection).

This insect seems to have been confused previously with *Stilpnotia parva*, Plötz (1880). The genitalia are distinct, and the fuscous streak on the discocellulars is much broader, approximately half a millemetre in *S. platyrhabda* as against half that measurement in *S. parva*.

Bazisa phaeophlebia, Hmpsn.

(Plate XII, fig. 6.)

Bazisa phaeophlebia, Hmpsn., Proc. Zool. Soc. Lond., **1910**: 455 (1910).

♀. Palpus, head and thorax capucine yellow, the thorax grading to pale orange yellow posteriorly. Antennal shaft pinkish buff, pectinations tawny olive. Abdomen benzo brown, mixed with pinkish buff at the junctions of the segments, the pale orange yellow of the thorax invading the basal segment; anal tuft sudan brown. Legs pinkish buff to pale orange yellow, mixed, especially on the outer side, with benzo brown. Pectus pinkish buff to capucine yellow. Venter benzo brown, mixed on the basal segments with capucine yellow, and with central and lateral longitudinal bands of capucine yellow. Wings pale pinkish buff, fringes somewhat lighter; costa of fore-wing edged with pinkish buff; veins of both wings, with the exception of the discocellulars, defined with fuscous as in the ♂, and a line of the same colour down the centre of the cell and also along the fold above the anal vein.

Expanse: ♀♀ 39–49 mm.

1 ♀ (neallotype) and 11 ♀♀, Lubudi, Belgian Congo, 5–13.iii.1923, *Ch. Seydel*; 2 ♀♀, Sandoa, S. E. Belgian Congo, 12.xii.1916 and 27.iii.1917, *F. G. Overlaet*; in the Musée du Congo Belge, Tervueren. 1 ♀, Mpika District, N. E. Rhodesia, 4000 ft., March–April 1921 (ex Joicey collection); 3 ♀♀, Tembura, South Sudan, December 1922 (ex Oberthür collection); 1 ♀, Ketoma, Uganda, 5000 ft., April 1923, *W. L. Doggett*; 2 ♀♀, Gondokoro, White Nile, *W. E. Reymes-Cole*. The last three specimens were cited as paratypes in the original description of *Laelia sericea*, Hmpsn. (1910), but evidently belong to the present species.

Leucoma brontonepha, sp. nov.

(Plate XIII, fig. 14.)

♂. Palpus xanthine orange, mixed with fuscous black above, the third segment entirely fuscous black. Antennal shaft fuscous black with a fine lateral white line; pectinations bone brown. Head sudan brown. Thorax fuscous black mixed with tawny olive; patagium sudan brown, fuscous black at base. Abdomen fuscous black mixed with tawny olive and cartridge buff, anal tuft capucine yellow. Legs fuscous black mixed with olive ochre and cartridge buff. Pectus sudan brown mixed with cartridge buff. Venter fuscous mixed with cartridge buff. Fore-wing velvety bone brown, irrorated over the whole wing, except in the discocellular and apical areas, with whitish and capucine yellow; a broad medial fascia of light cinnamon drab, its edges well defined, commencing at the upper angle of the cell, embracing the discocellulars, and obsolescent from the lower angle of the cell to the tornus; fringe bone brown. Hind-wing whitish; fuscous at the anal angle and along the termen, and strongly marked with velvety bone brown in the apical area, as far as the junction of veins $R5$ and $M1$ and the junction of $M3$ with the termen; fringe fuscous at anal angle, thereafter whitish, and bone brown in the apical area. Underside of fore-wing bone brown; basal half of costal margin marked with capucine yellow, especially above the discocellulars; the medial fascia of the upperside reproduced in whitish, but finishing at vein $Cu2$; fringe bone brown. Underside of hind-wing as on upperside.

Expanse: 51 mm.

1 ♂ (holotype) Antsianaka and Lake Alàotra, Madagascar, 2nd quarter 1889, *E. & B. Perrot* (ex Oberthür collection).

This insect resembles in facies *Leucoma vosseleri*, Grunb. (1907), with which it is evidently congeneric.

Naroma nigrolunata, sp. nov.

(Plate XII, fig. 2.)

♂. Palpus cartridge buff, bone brown on the outer and upper sides. Antennal shaft white, tipped with tawny olive; pectinations tawny olive. Head, thorax, legs and abdomen white to cartridge buff, the tibia and tarsus of fore-leg, and tibia of middle-leg, streaked with bone brown. Pectus and venter white to cartridge buff. Fore-wing white, the veins defined with cartridge buff; on the discocellulars a crescent-shaped spot with concavity apicad, of warm buff bordered heavily with bone brown; a broken line of bone brown along the lower margin of the cell; on the inner margin a broad patch of smoke grey; a series of preterminal bone-brown spots on the vein ends from *R*5 to *Cu*1; fringe at apex whitish, darkening gradually to smoke grey at the tornus. Hind-wing and fringe white. Underside of both wings white, with a spot of snuff brown at the base of the projection on the costa of the fore-wing. Fringes white.

♀. Resembles the ♂, but larger. In the allotype the preterminal spots on the fore-wing are augmented by spots at the vein ends of *R*4 and *Cu*2, and there is a tendency for the smoke grey to extend along the termen joining up the spots.

Expanse: ♂♂ 26–30 mm., ♀♀ 32–33 mm.

1 ♂ (holotype), 1 ♀ (allotype) and 2 ♂♂ (paratypes), Bitje, Ja River, Cameroons, October, wet season; also 1 ♂ and 1 ♀ (paratypes) from the same locality, 2000 ft., dry season. All collected by *G. L. Bates* (ex Joicey collection).

This insect resembles *Naroma signifera*, Wlkr. (1856), but is evidently distinct. A series of normal specimens of *N. signifera* is in the British Museum collection from Bitje, the type locality of *N. nigrolunata*. *N. nigrolunata* may be easily distinguished by the presence of the preterminal spots on the fore-wing and the dark border to the spot on the discocellulars.

Crorema submaculata, sp. nov.

(Plate XII, fig. 4.)

♂. Palpus antimony yellow. Antennal shaft light orange yellow at the base, grading to maize yellow at the tip; pectinations sayal brown. Head light orange yellow. Thorax light orange yellow on patagium and tegula, maize yellow mixed with light orange yellow posteriorly. Abdomen antimony yellow; dorsally on the basal segments some long bushy hair-scales of maize yellow. Legs with femora antimony yellow, tibiae and tarsi benzo brown, the inner side of hind-leg and spurs on mid- and hind-legs lighter. Pectus and venter antimony yellow. Fore-wing buff yellow, mixed with light orange yellow at the base; a series of eight benzo-brown spots placed interneurally; the first, which is very faint, between veins *R*4 and *R*5 and midway between the vein-stalk and the termen; the second, slightly more basad, between *R*5 and *M*1; the third, crescent-shaped with horns directed terminad, the upper longer than the lower, between *M*1 and *M*2 and close to the discocellulars; the fourth and fifth, short stripes between *M*2, M3 and *Cu*1, slightly nearer to the termen than to the cell; the sixth, a longer stripe, slightly curved, between *Cu*1 and *Cu*2 and at about one-third the distance from cell to termen; the seventh and eighth between *Cu*2 and the anal vein, below the origin of *Cu*2 with the cell and directed oblique inwardly; fringe buff yellow, darker interneurally. Hind-wing of a slightly lighter tint than the fore-wing; fringe buff yellow, darker interneurally. Fore-wing beneath buff yellow, the series of spots on upperside faintly reproduced; fringe as on upperside. Hind-wing beneath buff yellow; a series of spots, in somewhat the same positions as those on fore-wing, the last three obsolescent; fringe as on upperside.

♀. More pale than the ♂, the spots on the fore-wing larger and the four between veins *M*1 and *Cu*2 more or less crescent-shaped; the spots on the underside of hind-wing only faintly visible.

Expanse: ♂♂ 35–37 mm., ♀♀ 48–51 mm.

1 ♂ (holotype), 1 ♀ (allotype), 2 ♂♂ and 1♀ (paratypes), Masisi, Oso-Lowa watershed, N.W. Kivu, 4000 ft., forest with some grass, February 1924, wet season, *T. A. Barns* (ex Joicey collection).

Perhaps nearest to *Crorema adspersa*, H.-Sch. (1854), but distinguishable therefrom by the presence of the series of spots on the underside of hind-wing, also by the position of the two spots between *Cu*2 and the anal vein of the fore-wing, which in the present species are strongly oblique inwardly, while in *C. adspersa* they are almost at right angles to the inner margin.

In the B.M. collection are 2 ♂♂ from Kenya and 2 ♂♂ from Uganda which may belong to this species, but in the absence of adequate material I have not included them in the series.

Crorema nigropunctata, sp. nov.

(Plate XII, fig. 3.)

♂. Palpus deep chrome. Antennal shaft light orange yellow, pectinations tawny. Head and thorax deep chrome, the thorax somewhat lighter posteriorly. Abdomen cream buff. Legs, pectus and venter cream buff to deep chrome; fore-leg with a frontal patch of fuscous black on the basal half of the coxa, and the front of femur, tibia and tarsus light quaker drab; middle-leg with the front of tibia and tarsus light quaker drab. In some of the paratypes the fuscous black and light quaker drab are absent. Fore-wing buff yellow, with a series of seven rounded sooty-black spots placed interneurally, the first, rather faint, postmedially between veins *R*4 and *R*5, another, better defined and slightly more basad, between *R*5 and *M*1, another, almost touching the discocellulars, between *M*1 and *M*2, another, more distad and very small, between *M*2 and *M*3, and three others, arranged longitudinally, equisized, conspicuous and in line with each other, between *M*3, *Cu*1, *Cu*2 and the anal vein; fringe buff yellow. Hind-wing cream colour, fringe slightly darker. Wings beneath cream colour, the principal veins, termen and a broad band on the costa of each wing buff yellow; the three longitudinal dots are faintly visible on the fore-wing in fuscous, and in the holotype and two of the paratypes there are three broad longitudinal fuscous streaks between *R*4, *R*5, *M*1 and *M*2, that between *M*1 and *M*2 being the longest; fringes cream colour.

Expanse: ♂♂ 30–36 mm.

1 ♂ (holotype) and 4 ♂♂ (paratypes), Okahandja, S. W. Africa, January and February 1928, *R. E. Turner*. Also 1 ♂ (paratype), S. W. Africa (ex Joicey collection).

In *Crorema nigropunctata* the spots on the upperside of fore-wing are black, small, rounded and distinct, and the three below the cell are in line with each other. In *C. adspersa*, H.-Sch. (1854), and *C. setinoides*, Holl. (1893), the spots are more irregular in shape, less distinct, and hair brown to fuscous in colour. In *C. adspersa* the three spots below the cell are not in line, and in *C. setinoides* there are two spots between *Cu*2 and the anal vein. In *C. evanescens*, Hmpsn. (1910), from the White Nile and Uganda, the spots are large and indistinct.

Crorema crocipes, Boisd.

(Plate XII, fig. 8.)

Crorema crocipes, (1833), Boisd., Faun. Madag. p. 87.

♂. Palpus capucine yellow. Antennal shaft white, basal segment capucine yellow, pectinations fuscous. Frons and vertex of head capucine yellow, occiput white. Thorax and abdomen white, the hair-scales so thinly placed that the chitin of the body surface is visible. Fore-leg capucine yellow, mid- and hind-leg somewhat lighter. Pectus and venter white, the hair-scales thinly placed. Wings semi-hyaline, white; the subcostal area of the fore-wing more thickly scaled, and opaque; fringes white. Underside of both wings, and fringes, white.

Expanse: ♂♂ 44–47 mm.

1 ♂ (neallotype), 46 ♂♂ and 6 ♀♀, Isle Sainte Marie de Madagascar, October–December 1896, *Perrot Frères*; also 11 ♂♂ and 2♀♀, between Isokitra and Diego Suarez, N. Madagascar, May–October 1891, *E. & B. Perrot* (all ex Oberthür collection).

The ♀♀ of this series agree well with the original holotype ♀ of Boisduval, which is in the B.M. collection. Neither sex has any trace of yellow at the base of costa of fore-wing. The antenna of the ♂ measures about 10 mm., and the pectinations have an uneven and bushy appearance. Palpus with two segments.

Redoa mayotta, sp. nov.

(Plate XII, fig. 1.)

♂. Palpus pinkish buff. Antennal shaft cartridge buff, pectinations somewhat darker. Head, thorax, abdomen and legs cartridge buff, the inner side of fore-leg tinged with Prout's brown. Wings and fringes, above and beneath, white; base of costa of fore-wing, for a distance of about 4 mm., faintly tinged with pinkish buff.

♀. Resembles the ♂, but the antenna with shorter shaft and pectinations, fore-wing longer and less broad, fore-leg and fore-wing without the Prout's brown and pinkish buff.

Expanse: ♂♂ 34–42 mm., ♀♀ 40–46 mm.

1 ♂ (holotype), 1 ♀ (allotype), 14 ♂♂ and 3 ♀♀ (paratypes), Mayotte Island, 1884, *L. Humblot*; 13 ♂♂ and 1 ♀, Comoro Islands, 1884–86, *L. Humblot* (all ex Oberthür collection).

Resembles *Redoa melanocraspis*, Hmpsn. (1905), but without the black border at the base of costa, and with antennal shaft and pectinations of ♂ slightly longer. The average wing-expanse of the present species is also greater.

Redoa xanthoma, sp. nov.

(Plate XII, fig. 9.)

♂. Palpus capucine yellow. Antennal shaft white, basal segment capucine yellow, pectinations fuscous. Frons and vertex of head capucine yellow, occiput white. Thorax and abdomen white, the hair-scales so thinly placed that the chitin of the body surface is visible. Fore-leg capucine yellow, mid- and hind-leg somewhat lighter. Pectus and venter white, the hair-scales thinly placed. Wings semi-hyaline, white; the subcostal area of the fore-wing more thickly scaled, and opaque; base of costa of fore-wing for a distance of about 4 mm. narrowly edged with capucine yellow; fringes white. Underside of both wings, and fringes, white; the capucine yellow edging to the base of costa of fore-wing extends narrowly to the underside.

Expanse: ♂♂ 40–48 mm.

1 ♂ (holotype) and 69 ♂♂ (paratypes), between Isokitra and Diego Suarez, N. Madagascar, May–October 1891, *E. & B. Perrot*; 7 ♂♂, Antsianaka Forest, Madagascar, 1888, *L. Humblot*; also 4 ♂♂, Tamatave and Alahakato Forests, 1st quarter, 1888, *Edouard Perrot* (all ex Oberthür collection).

This insect is similar in appearance to *Crorema crocipes*, Boisd. (1833), but can be distinguished at once by the ♂ antenna, which in the present species measures 8–9 mm. and has an even appearance, with pectinations parallel to one another; also by the presence of the yellow edging to the base of costa of fore-wing, and by the considerably longer palpus, which has three segments.

Redoa kenya, sp. nov.

(Plate XII, fig. 21.)

♂. Palpus whitish, mixed on the outer side with fuscous. Antennal shaft white, pectinations pinkish buff. Frons cream colour, remainder of head white mixed with cream colour.

Abdomen white, thinly haired. Legs whitish; fore-leg marked on the inner side, excepting the last segments of the tarsus, with clove brown, the process on the tibia tawny olive and strongly curved towards the tip; middle leg marked on the inner side of tibia with clove brown. Pectus and venter whitish. Wings white, semi-hyaline, iridescent in certain lights; costa of fore-wing, on the basal one-fifth, strongly edged with fuscous black; fringes white. Underside of both wings white, iridescent in certain lights; traces of fuscous shading at the apex of the fore-wing; fringes white.

♀. Resembles the ♂, but the fuscous-black edging on the costa of the fore-wing somewhat reduced in length.

Expanse: ♂♂ 47–51 mm., ♀♀ 54–56 mm.

1 ♂ (holotype), 1 ♀ (allotype), 2 ♂♂ and 1 ♀ (paratypes), S.E. slopes of Mt. Kenya, 5000–7000 ft., February 1911, *S. A. Neave*; 3 ♂♂ (paratypes), E. foot and slopes of Aberdare Mountains, British E. Africa, 7000–8500 ft., February 1911, *S. A. Neave.*

Olapa ituri, sp. nov.

(Plate XII, fig. 17.)

♂. Palpus and head light orange yellow. Antennal shaft light orange yellow at base, grading distally to cartridge buff, and marked with fuscous; pectinations fuscous. Thorax drab, patagium light orange yellow, Abdomen light orange yellow. Legs pale orange yellow, mixed on tibiae and tarsi with fuscous. Pectus and abdomen light orange yellow. Wings semi-hyaline; fore-wing drab; basal half of costal margin thinly marked with fuscous; a conspicuous fuscous spot in the angle between vein *Cu*2 and the cell, not touching the veins; fringe slightly darker than the fore-wing, except at the ends of the veins. Hind-wing and fringe drab, of a slightly lighter tint than the fore-wing; in certain lights both wings are iridescent. Underside of both wings drab, iridescent in certain lights; fringes drab.

♀. Resembles the ♂, but somewhat more pale. The light orange yellow of the patagium extends to the tegula, and there is no fuscous marking on the antennal shaft and hind-leg.

Expanse: ♂ 38 mm., ♀ 48 mm.

1 ♂ (holotype), Eastern Upper Ituri Valley, 30 miles south of Irumu, Belgian Congo, 3000 ft., tropical forest, July 1924; 1 ♀ (allotype), Ituri Forest, Congo-Semliki watershed, 3 days south of Irumu, Belgian Congo, February 1920, *T. A. Barns* (ex Joicey collection).

There is a very small aborted proboscis.

Olapa leptomita, sp. nov.

(Plate XII, fig. 15.)

♂. Palpus, head and thorax cartridge buff to warm buff. Antennal shaft cartridge buff, pectinations fuscous. Abdomen warm buff, basal segments whitish. Legs, pectus and venter warm buff; some fuscous shading on the inner side of fore- and mid-legs. Wings semi-hyaline; fore-wing whitish, costal area tinged with cartridge buff; costal margin from base to apex distinctly edged with fuscous; a fuscous spot in the angle between vein *Cu*2 and the cell, not touching the veins; fringe whitish. Hind-wing and fringe whitish. Underside of both wings whitish, iridescent in certain lights; fringes whitish.

♀. Wings more thinly scaled than in the ♂, and slightly longer in proportion to breadth. There is no fuscous on the legs. The fuscous edging to the costal margin of the fore-wing is indistinct and extends only to the basal one-third of the margin.

Expanse: ♂♂ 38–41 mm., ♀ 50 mm.

1 ♂ (holotype) and 1 ♂ (paratype), Tero Forest, S.E. Buddu, Uganda, 3800 ft., 27.ix.1911; 1 ♀ (allotype), Mpanga Forest, Toro, Uganda, 4800 ft., 14.xi.1911, *S. A. Neave.*

May be placed next to the preceding species.

Lacipa tau, sp. nov.

(Plate XII, fig. 20.)

♂. Palpus capucine yellow. Basal one-third of antennal shaft pale pinkish buff, remainder verona brown mixed with pale pinkish buff; pectinations verona brown. Head pale pinkish buff mixed with orange buff. Thorax orange buff, with some fuscous-black hair-scales centrally and at the base of the tegula. Abdomen orange buff, each segment basally edged across the dorsal area with fuscous black. Fore- and middle-legs pale pinkish buff mixed with orange buff and fuscous black, hind-leg orange buff. Pectus pale pinkish buff tinged with orange buff. Venter orange buff, each segment basally edged with fuscous black more broadly than on the upperside. Fore-wing pale pinkish buff, somewhat lighter between the veins; sparse fuscous-black irroration over the whole wing, almost absent below the cell and in the costal area from antemedial fascia to apex; a capucine yellow spot subbasally in the cell; a small fuscous-black spot below the cell between subbasal and antemedial areas; a T-shaped antemedial fascia made up of six interneural spots of capucine yellow, the first three strongly oblique outwardly, the third situated just above the junction of vein *Cu*2 with the cell, the last three forming the stem of the T and slightly oblique inwardly to the inner margin; a group of four fuscous-black spots, one inside the upper angle of the cell, another between veins *M*1 and *M*2 almost touching the discocellulars, two others between veins *M*2, *M*3 and *Cu*1 close to the postmedial fascia on its proximal side; a postmedial fascia made up of interneural spots of capucine yellow, commencing just before the apex and running to the inner margin at two-thirds, with a slight curve inwards between veins *M*2 and *Cu*1; a preterminal series of interneural fuscous-black spots; fringe pale orange yellow. Hind-wing and fringe orange buff; a preterminal series of interneural fuscous-black spots, not reaching the anal angle. Underside of fore-wing orange buff, mixed with fuscous over the whole wing except for a narrow strip along the termen and more broadly along the inner margin; a preterminal series of fuscous-black spots, not reaching the tornus; fringe orange buff. Underside of hind-wing and fringe orange buff, rather darker than on upperside; a fuscous-black spot in the angle formed by the stalk of *R*5 and *M*1 with the discocellulars; a preterminal series of fuscous-black spots.

Expanse: ♂♂ 28–29 mm.

1 ♂ (holotype) and 2 ♂♂ (paratypes), Ngorongoro Crater, Arusha District, Tanganyika Territory, 5800 ft., February 1921, open grass country, *T. A. Barns* (ex Joicey collection).

Probably nearest to *Lacipa sarcistoides*, Her. (1926).

Euproctis ouria, sp. nov.

(Plate XII, fig. 10.)

♂. Palpus Sanford's brown, tipped with yellow ochre. Antennal shaft Naples yellow, pectinations ochraceous tawny. Head yellow ochre, the eye surrounded with Sanford's brown. Thorax and abdomen yellow ochre, tegula long and rather bushy. Legs yellow ochre, tibiae and tarsi tinged with Sanford's brown. Pectus and venter yellow ochre, pectus in front Sanford's brown. Fore-wing mustard yellow; a tinge of Sanford's brown along the base of the costa; a Sanford's brown antemedial fascia, broken at the veins, commencing on the upper margin of the cell at one-half and curving outwardly to the junction of *Cu*2 with the cell, thence inwardly oblique to the inner margin at one-quarter; a large circular spot of Sanford's brown on the upper half of the discocellulars; a postmedial fascia of Sanford's brown, broken at the veins, commencing just beyond the origin of *R*5, parallel with the termen to *M*3, thence inwardly oblique to the inner margin at one-half; a subterminal series of interneural Sanford's brown spots, that between *M*1 and *M*2 prolonged basad into a short streak, and the two between *Cu*1, *Cu*2 and the anal vein situated slightly more basad than the remainder; fringe mustard yellow. Hind-wing cartridge buff, fringe slightly darker. Underside of both wings cartridge buff, suffused towards the termen with straw yellow; costa of fore-wing tinged with yellow ochre, and a faint spot of yellow ochre on the discocellulars of both fore- and hind-wing; fringes straw yellow.

Expanse: ♂♂ 32–39 mm.

1 ♂ (holotype) and 1 ♂ (paratype), Virunga Mountains, Lake Kivu, 9000 ft., October 1921; 3 ♂♂ (paratypes), Rugege Forest, Ruanda District, Lake Kivu, 7000 ft., December 1921; 1 ♂ (paratype), Mt. Mikeno, N. Kivu, 7500 ft., September 1919; 1 ♂ (paratype), Kisiba, Bugoie Forest, W. Kivu, 8500 ft., November 1921. All collected by *T. A. Barns* (ex Joicey collection).

This fine mountain species is very distinct from any other *Euproctis*, but may perhaps be ranged near to *E. fasciata*, Wlkr. (1855).

Euproctis turificator, sp. nov.

(Plate XII, fig. 11.)

♂. Palpus Sanford's brown, third segment cartridge buff. Antennal shaft cartridge buff, pectinations ochraceous tawny. Head and thorax light orange yellow to capucine yellow, the eye edged below and on the outer side with Sanford's brown. Abdomen cream colour, with some long and bushy light orange-yellow hair-scales on the basal segments. Pectus, venter and legs cartridge buff to cream colour, the tibiae and tarsi with long and bushy hair-scales of cream colour to light orange yellow. Fore-wing cream colour mixed somewhat irregularly with light orange yellow; a medial fascia of burnt sienna, reaching from the middle of the cell to the inner margin, and filling up the space between the antemedial and postmedial, which except for a faintly marked bow of Sanford's brown (concavity basad) from the costa to vein *Cu*1, are not evident; the proximal edge of the medial fascia is almost straight, and at right-angles to the inner margin, the distal edge inwardly oblique to a point midway between *Cu*2 and the anal vein, thence outwardly oblique to the inner margin; on the upper half of the discocellulars a large rounded spot of Sanford's brown, touching the upper end of the medial fascia; beyond the medial fascia a light sinuous band indicated by a decrease in the light orange yellow, followed by another sinuous band in which this colour predominates; a subterminal Sanford's brown spot between veins *M*1 and *M*2, and a double spot of the same colour between *Cu*2 and the anal vein; some long spatulate fuscous-black hair-scales along the inner margin; fringe cream colour. Hind-wing cartridge buff, with some long cream-colour hair-scales between the cell and the inner margin; fringe cream colour. Underside of both wings ivory yellow; costa of both wings and fringes somewhat darker; a faint spot of capucine yellow on the discocellulars of the fore-wing.

♀. Resembles the ♂, but larger and paler; final segments of abdomen and anal tuft ochraceous tawny; medial fascia of fore-wing carob brown; three additional subterminal Sanford's brown spots, between veins *R*4 and *R*5, *M*2 and *M*3, and *Cu*1 and *Cu*2.

Expanse: ♂♂ 38–39 mm., ♀ 53 mm.

1 ♂ (holotype), 1 ♀ (allotype) and 1 ♂ (paratype), Rugege Forest, Ruanda District, Lake Kivu, 7000 ft., December 1921; 1 ♂ (paratype), Kivu-Oso Watershed, N.W. Kivu, 4500–6000 ft., September 1921, *T. A. Barns*; also 1 ♂ (paratype), lava plains beneath Birunga Volcanoes, between Lakes Kivu and Edward, 5000 ft., March–April 1924, *Mrs. T. A. Barns* (all ex Joicey collection).

This species may be ranged near to *Euproctis torrida*, Dist. (1897). Its name has been chosen in consequence of a fancied resemblance of the markings on the fore-wing to a cowled figure, seen in profile, bearing a smoking lamp.

Euproctis hargreavesi, sp. nov.

(Plate XII, fig. 7.)

♂. Palpus cartridge buff, the first and second segments above and on the outer side capucine yellow. Antennal shaft cartridge buff, pectinations cinnamon buff. Head capucine yellow, mixed on the frons with cream colour. Thorax cream colour, mixed behind the head with capucine yellow. Abdomen white, dorsally on the basal segments cream colour; anal tuft cream colour. Legs white to cartridge buff, fringed with long cream-colour hair-scales. Pectus and venter white to cartridge buff. Fore-wing white, marked with patches of delicate cream colour in the basal area and along the costa, also neurally in the postmedial, subterminal and terminal areas; these patches may disappear in worn specimens, and are absent in two of the paratypes; medially on the inner marginal area an irroration of fuscous-black scales mixed with a few of capucine yellow; a fuscous-black spot at the centre of the discocellulars; a series of subterminal interneural fuscous-black spots, obsolescent between veins *M*3, *Cu*1 and *Cu*2, the two between *Cu*2 and the anal vein somewhat further from the termen; fringe whitish, tipped with cream colour. Hind-wing whitish; inner marginal area with some long cartridge buff hair-scales; fringe cartridge buff. Underside of fore-wing white, basal half of costal area cream colour; fringe white tipped with cream colour. Underside of hind-wing white; fringe white tipped with cartridge buff.

♀. Very similar to the ♂, but the capucine yellow is absent on the thorax and nearly so on the head. The abdomen is thinly scaled, and the dark-coloured chitin of the body surface is visible at the junctions of the segments; anal tuft large, amber brown.

Expanse: ♂♂ 31–36 mm., ♀♀ 46–50 mm.

1 ♂ (holotype), larva on *Cajanus indicus*, 26.iv.1930; 1 ♀ (allotype), on *Erythrina*, 5.i.1928; 1 ♂ (paratype), 14.v.30, larva on *Bridelia micrantha*, and 1 ♂ (paratype), 19.x.1929, all Kampala, Uganda, *H. Hargreaves*; 1 ♀, 17.v.1910, Entebbe, Uganda, *C. C. Gowdey*. All presented by the Imperial Institute of Entomology.

Euproctis ceramozona, sp. nov.

(Plate XII, fig. 19.)

♂. Palpus fuscous, beneath and terminally light orange yellow. Antennal shaft light orange yellow to orange buff, pectinations honey yellow. Head orange buff, the frons light orange yellow. Thorax orange buff, dorsally and in the tegula some long and upstanding spatulate fuscous scales. Abdomen orange buff to light orange yellow, cartridge buff at the base. Legs, pectus and venter light orange yellow to orange buff, the pectus in front fuscous black, the legs with fringes of bushy hair-scales which are mainly apricot yellow. Fore-wing apricot yellow; a very broad medial band of interneural fuscous irroration, mixed with a few scales of xanthine orange, occupying more than a third of the lower half of the wing, produced proximally into the cell and distally towards the apex, which it does not quite reach; along the inner margin some long upstanding spatulate fuscous scales, not entirely confined to that part of the margin touched by the median band; a small patch of interneural irroration subterminally between veins *M*2 and *M*3, also between *Cu*1 and *Cu*2; fringe buff yellow. Hind-wing cartridge buff, tinged with light orange yellow in the inner marginal area; fringe buff yellow. Wings beneath cartridge buff, costa of fore-wing orange buff; fringes buff yellow.

♀. The head and thorax, fore-wing and fringe, and fringe of hind-wing, are pale orange yellow mixed with light ochraceous buff; the markings of fore-wing are similar to those of the ♂, but the irroration more widely spaced, and an additional subterminal patch of irroration between veins *M*3 and *Cu*1, also between *Cu*2 and the anal vein.

Expanse: ♂♂ 37 and 38 mm., ♀ 52 mm.

1 ♂ (holotype) and 1 ♀ (allotype), Ilesha, S. Nigeria, *L. E. H. Humfrey*; 1 ♂, Sekondi, Gold Coast (ex Joicey collection).

Euproctis jefferyi, sp. nov.

(Plate XII, fig. 12.)

♂. Palpus capucine yellow. Antennal shaft cartridge buff irrorated with Saccardo's umber; pectinations tawny olive. Head capucine yellow, posteriorly pinkish buff, and with a band of Saccardo's umber between the antennae. Thorax capucine yellow, cartridge buff posteriorly; patagium Saccardo's umber; tegula rather long, clove brown basally, capucine yellow medially, and tipped with clove brown. Abdomen argus brown, the distal ends of the posterior segments edged with cinnamon buff; anal tuft cinnamon buff. Legs Saccardo's umber, mixed on fore- and middle-legs with fuscous and Isabella colour. Pectus and venter cartridge buff, the posterior half of venter sepia. Fore-wing with ground-colour cartridge buff, covered thickly but irregularly with scales of yellow ochre mixed with maize yellow; a small streak of clove brown subbasally; costa narrowly edged with Saccardo's umber; three rounded fuscous-black spots at the discocellulars, two placed just within the cell, and the third beyond it between veins *M*1 and *M*2; an inwardly oblique stripe of bistre (absent in some of the paratypes) running from the apex to a point on vein *M*2 midway between the cell and termen, thereafter obsolescent; a preterminal series of well-defined interneural fuscous-black spots; fringe maize yellow. Hind-wing cartridge buff, fringe slightly darker. Underside of fore-wing Saccardo's umber; fringe maize yellow with a slight admixture of Saccardo's umber. Underside of hind-wing cartridge buff, shading towards the costa to Saccardo's umber; fringe maize yellow.

♀. Resembles the ♂, but considerably paler, and the oblique stripe on the fore-wing barely visible. Anal tuft cinnamon buff mixed with fuscous black. Underside of both wings and fringes cartridge buff.

Expanse: ♂♂ 28–29 mm., ♀♀ 26–29 mm.

1 ♂ (holotype), 1 ♀ (allotype), 4 ♂♂ and 1 ♀ (paratypes), Kitali, Kenya, April 1926 and 1927, *G. W. Jeffery* (ex Joicey collection).

Resembles in facies *Euproctis flavitincta*, Hmpsn. (1910), but, among other differences, lacks the yellow antemedial and postmedial lines. There is no areole, and vein *R*1 rises from the cell at about six-sevenths. A short, aborted proboscis is present.

Neomardara divergens, sp. nov.

(Plate XIII, fig. 11.)

♂. Palpus tawny olive. Antenna Prout's brown, mixed with white on basal half of shaft. Head and thorax Prout's brown, a band of white across the patagium towards its posterior edge, basal half of tegula mainly white. Abdomen tawny olive mixed with Prout's brown, anal tuft tawny olive. Fore-leg Prout's brown, mixed on the coxa with whitish; middle-leg tawny olive, the tarsus shaded with fuscous; hind-leg tawny olive. Pectus and venter tawny olive, the pectus mixed with Prout's brown and whitish. Fore-wing Prout's brown, darker at the base and along the costa; a patch of pinkish buff at the base of the inner margin; a band of white, commencing broadly at the middle of the subbasal area, narrowing throughout its length and finishing at the middle of the costa, the side towards the costa irrorated with cinnamon buff; a band of buffy brown, bordered on each side by whitish, running in the subterminal area from apex to inner margin, broadening throughout its length, the distal margin parallel with the termen, at the inner margin turning basad and running without white borders almost to the base of the wing; the area between veins *M*2 and *Cu*1, from the lower margin of the cell to the postmedial fascia, filled in with white lightly irrorated with buffy brown; below the junction of vein *Cu*2 with the cell a square-ended patch of white running terminad and finishing at the buffy-brown area; a faint Prout's brown subterminal fascia, broken at the veins and parallel with the termen; between the subterminal fascia and the termen some white interneurally; termen edged with pinkish buff; fringe fuscous. Hind-wing pinkish buff, some fuscous irroration in the terminal area and more broadly in the apical area; fringe fuscous mixed with pinkish buff. Underside of fore-wing Prout's brown to buffy brown, the white markings of the upperside faintly reproduced in whitish to pinkish buff; termen edged with pinkish buff; fringe fuscous. Underside of hind-wing pinkish buff, marked in an irregular manner between the upper margin of the cell, vein *M*1 and the costa with Prout's brown; termen edged with pinkish buff; fringe fuscous mixed with pinkish buff.

Expanse : 36 mm.

1 ♂ (holotype), Solwezi, N.W. Rhodesia, 1.xi.1917, *H. C. Dollman.*

This species can be easily distinguished from *Neomardara africana*, Holl. (1893), by the position of the two white lines on the distal area of the fore-wing, which are roughly parallel with the termen in *N. africana*, while in the present species they diverge evenly from each other throughout their length.

It may be of interest to call attention to the resemblance between the species of this African genus and members of the genus *Lepasta*, Möschl. (NOTODONTIDAE), of South America.

Pirga cryptogena, sp. nov.

(Plate XIII, fig. 1.)

♂. Palpus short, bone brown. Antennal shaft bone brown, the basal segment pale orange yellow; pectinations fuscous black. Head and thorax bone brown, patagium, tegula and posterior end of thorax deep chrome, this colour extending also over the extreme base of the fore-wing. Abdomen bone brown, with a lateral band of deep chrome, and each segment edged posteriorly with light orange yellow. Pectus and legs bone brown, with a tuft of deep chrome hair-scales at the trochanter of the hind-leg. Venter bone brown, with a few scattered deep chrome hair-scales on each segment posteriorly. Fore-wing with basal half pearl grey and translucent; distal half semi-hyaline with a thick irroration of cinnamon-buff and bone-brown scales, giving a " brown " appearance which varies in shade according to the way in which it is viewed. The division between the basal and distal areas runs from the junction of *R*1 with the cell, through the junction of *Cu*1 with the cell, to the inner margin at three-quarters. The area between the subcostal vein and the costa is also included in the " brown " area. Veins over the whole wing bone brown. The pearl-grey area is reduced in a few of the paratypes, the line of demarcation running through the junction of *Cu*2 with the cell. Hind-wing coloured similarly to fore-wing, the line of demarcation running through the stalk of *R*5 and *M*1, through *M*2 and *M*3 near their point of origin, to the inner margin at three-quarters. The pearl-grey area is reduced in some of the paratypes, the " brown " area reaching the discocellulars. Underside of both wings similar to upperside.

Expanse : ♂♂ 53–66 mm., with a single dwarfed specimen of only 46 mm.

1 ♂ (holotype) and 44 ♂♂ (paratypes), Daro Forest, Toro, Uganda, 4000–4500 ft., 25–29.x.1911; also 1 ♂ (paratype), W. shores of Victoria Nyanza, Buddu, Uganda, 3700 ft., 25.ix.1911. All collected by Dr. S. A. Neave.

These insects have a well-developed frenulum, remarkable for the fact that, in a number of specimens, it is divided into three spines of approximately equal length. Although the frenulum might thus be mistaken for that of a ♀, the series is undoubtedly composed of ♂♂, as evidenced by the antennae and genitalia. There is also a short, aborted proboscis.

Resembles *Pirga magna*, Swinh. (1903), but is much smaller, and the pearl-grey area of the hind-wing reduced in extent.

Marbla lutulenta, sp. nov.

(Plate XII, fig. 16.)

♂. Palpus, head, thorax, abdomen and legs light orange yellow; process on the fore-leg longer than the tibia, and for three-quarters of its length approximately as broad as the tibia. Antennal shaft light orange yellow, grading to cartridge buff towards the tip, pectinations bistre. Wings semi-hyaline; fore-wing and fringe drab; hind-wing and fringe light drab; underside of both wings similar to upperside, fringes somewhat lighter.

Expanse: ♂♂ 34–37 mm.

1 ♂ (holotype) and 2 ♂♂ (paratypes), Bitje, Cameroons, May and June, wet season (ex Joicey collection).

Marbla coelebs, sp. nov.

(Plate XII, fig. 14.)

♂. Palpus, head and thorax pinkish buff, the tip of the palpus darker. Antennal shaft hair brown, pectinations somewhat darker. Basal segments of abdomen pinkish buff mixed with hair brown, distal segments hair brown, anal tuft drab. Legs, pectus and venter pinkish buff, the fore-leg with some bistre on the inner side, especially on the tibia and tibial process. Wings translucent, iridescent in certain lights. Fore-wing hair brown, the veins and fringe more densely scaled and therefore darker. Hind-wing and fringe whitish. Underside of fore-wing and fringe, hair brown; of hind-wing, whitish.

Expanse: ♂♂ 29–34 mm.

1 ♂ (holotype) and 4 ♂♂ (paratypes), Upper Lowa Valley, near Masisi, W. Kivu, 5000–6000 ft., forest and long grass, February 1924, wet season, *T. A. Barns* (ex Joicey collection). Also 1 ♂, Tero Forest, S.E. Buddu, Uganda, 3800 ft., 30.ix.1911, *S. A. Neave.*

Laelia eutricha, sp. nov.

(Plate XIII, fig. 5.)

♂. Palpus and head warm sepia, thorax verona brown. Antennal shaft cartridge buff, pectinations fuscous, the amber-brown colour of the bristles at the end of each pectination giving a "reddish" tinge to the tips. Abdomen drab, tinged with verona brown. Legs, pectus and venter warm sepia. Fore-wing drab tinged with verona brown, irrorated throughout with fuscous black; on each side of the lower half of the discocellulars the irroration is increased, making a faintly seen longitudinal shade which does not reach the base of the wing; a subterminal fascia of interneural fuscous-black spots, commencing between veins *R*5 and *R*4, roughly parallel with the termen to below vein *M*2, the spot between *M*3 and *Cu*1 closer to the termen, thence inwardly oblique to below vein *Cu*2; fringe drab. Hind-wing cartridge buff shaded with drab; a subterminal fuscous spot between vein *Cu*2 and the 2nd anal; fringe drab. Underside of both wings drab to verona brown, apex and costal area darker and sparsely irrorated with fuscous black; fringes drab.

♀. Resembles the ♂, but the fore-wing is narrower, the termen more oblique and the markings reduced. In the allotype ♀ the markings are visible, but in the paratype ♀ they cannot be distinguished.

Expanse: ♂♂ 33–37 mm., ♀♀ 37–42 mm.

1 ♂ (holotype) and 2 ♂♂ (paratypes), April 1926 and 1927; 1 ♀ (allotype) and 5 ♂♂ (paratypes), March 1927 and 1930; 1 ♂ (paratype), July 1925; 1 ♀ (paratype), August 1925; all Kitale, Kenya, *G. W. Jeffery* (ex Joicey collection). Also 1 ♂, Lumbwa, British East Africa, October 1921, *G. W. Jeffery*; and 1 ♂, Kampala, Uganda, 12.viii.1929, *H. Hargreaves.*

May be distinguished from *Laelia bifascia*, Hmpsn. (1905), by, among other differences, the almost complete absence of the two longitudinal stripes on the fore-wing. In *Laelia lavia*, Swinh. (1903), the last two spots of the subterminal fascia are roughly midway between cell and tornus; in the present species they are considerably nearer to the tornus.

Dasychira aethalodes, sp. nov.

(Plate XIII, figs. 2 & 3.)

♂. Palpus bone brown, lighter above and tipped with cartridge buff. Antennal shaft bone brown, sparsely irrorated with cartridge buff; pectinations buckthorn brown. Head and thorax bone brown. Abdomen bone brown finely streaked with cartridge buff, a patch of lighter hair-scales laterally on the basal segments, dorsal tufts of glossy bone brown on the basal segments, and the anal tuft clove brown mixed with mummy brown. Fore and middle legs bone brown, covered with long hair-scales; hind-leg less heavily haired, Saccardo's umber mixed with bone brown. Pectus and venter Saccardo's umber mixed with mummy brown. Fore-wing clove brown; a patch of cartridge buff between the base of the anal vein and the inner margin; an indistinct subbasal fascia of bone brown, bowed (concavity basad) from costa to just above anal vein, thence outwardly oblique to inner margin; a reniform composed of two bone-brown crescent-shaped lines with concavities terminad, each crescent broken just below its upper tip; a crenulate bone-brown postmedial fascia, irregularly bowed (concavity basad) from the costa to vein *Cu*1, thence at right angles to inner margin; an indistinct, broad and irregular subterminal fascia, roughly parallel with the postmedial, bone brown mixed with drab; a bone-brown preterminal fascia, more regular than the others but broken on the veins; fringe clove brown, with a lighter line at its base and tipped at the vein ends with cartridge buff. Hind-wing cartridge buff, tinged with cream buff along the inner margin; preterminal area shaded with mummy brown, and a narrow terminal line of the same colour; fringe cartridge buff shaded with mummy brown interneurally. In the type and most of the paratypes the mummy brown does not reach the anal angle, and in other paratypes is almost or entirely absent. Underside of fore-wing cartridge buff, heavily irrorated, except between vein *Cu*2 and the inner margin, with mummy brown; the irroration increases towards the costa, and also forms an indistinct spot on the discocellulars and a postmedial streak between the costa and vein *R*5. Fringe clove brown, cartridge buff at the vein ends. Underside of hind-wing cartridge buff, with slight mummy-brown irroration in the costal, preterminal and apical areas, and a spot in the centre of the discocellulars. Fringe cartridge buff, mummy brown interneurally.

♀. Resembles the ♂, but considerably larger. The fore-wing has a rather lighter and more unicolorous appearance, the hind-wing shaded throughout with mummy brown, slightly more heavily on the veins. Underside of both wings shaded throughout with mummy brown, a straight postmedial fascia across both wings, and a discocellular spot on the hind-wing.

Expanse: ♂♂ 42–44 mm., ♀♀ 46–53 mm.

1 ♂ (holotype), 1 ♀ (allotype), 12 ♂♂ and 16 ♀♀ (paratypes), 10th June–10th July 1913; 1 ♀ (paratype), 25th March 1913; 1 ♂ (paratype), 19th May 1913;

1 ♂ and 1 ♀ (paratypes), December 1913; 1 ♀ (paratype), 3rd January 1914; all Mt. Mlanje, Nyasaland, *S. A. Neave.* Also 1 ♀, Kashitu, N.W. Rhodesia, 7th May 1915, *H. C. Dollman.*

May be ranged next to *Dasychira goodii*, Holl. (1893).

Dasychira elaeochroa, sp. nov.

(Plate XIII, fig. 4.)

♂. Palpus drab, with a line of bistre laterally on the outer side. Antennal shaft bistre, pectinations fuscous. Head bistre, mixed on the frons with whitish. Thorax bistre, the tegula mixed with whitish. Abdomen pale pinkish buff mixed with drab, anal tuft slightly darker, dorsal tufts bistre. Fore-leg bistre mixed with pale pinkish buff, tarsus bistre ringed with pinkish buff; middle-leg bistre mixed with pale pinkish buff; hind-leg pale pinkish buff, the tarsus marked with bistre. Pectus and venter pale pinkish buff to pinkish buff, the former mixed with bistre. Fore-wing fuscous mixed in varying proportions with dull citrine and whitish, the dull citrine predominating between the anal vein and the inner margin, in the cell, and on the distal two-fifths of the wing; a patch of pale pinkish buff at the base of the inner margin; an irregular fuscous-black subbasal fascia; a broad, sinuate, fuscous-black antemedial fascia, almost at right-angles to the inner margin, its edges merged into a patch of fuscous black between the cell and the anal vein; a crenate fuscous-black postmedial fascia, points on the veins, concavities terminad, bowed (concavity basad) from costa to vein *Cu*1, directed basad for a short distance along *Cu*1, thence inwardly oblique to the inner margin; two whitish spots, joined by a narrower streak, between vein *Cu*2 and the inner margin, midway between the postmedial and the preterminal; a faint fuscous preterminal fascia, broken at the veins; fringe fuscous, at the vein-ends drab. Hind-wing cartridge buff, the veins shaded with pale pinkish buff; a few fuscous scales at the apex; fringe whitish, mixed with fuscous at the apex, and with a line of pale pinkish buff at its base. Fore-wing beneath cartridge buff, lightly shaded along costa and towards termen with fuscous; a broad straight postmedial fascia formed by an increase in the fuscous shading; fringe fuscous, drab at the vein-ends. Underside of hind-wing and fringe as on upperside, with additional fuscous marking along the distal two-thirds of the costa.

♀. Resembles the ♂ in pattern and general appearance, but the abdomen is of a darker shade, and the hind-wing above and beneath shaded lightly throughout with fuscous.

Expanse: ♂ 38 mm., ♀♀ 45–48 mm.

1 ♂ (holotype), 30.vi.1915, 1 ♀ (allotype), 9.vi.1915, and 1 ♀ (paratype), 16.vi.1915; all from Kashitu, N.W. Rhodesia, *H. C. Dollman.*

Dasychira triselena, sp. nov.

(Plate XIII, fig. 15.)

♀. Palpus tawny olive mixed with fuscous. Antennal shaft cartridge buff at base, shading to snuff brown distally; pectinations snuff brown. Head white, beneath and behind the eye tawny olive mixed with fuscous. Thorax and abdomen tawny olive mixed with cartridge buff. Fore-leg tawny olive mixed with fuscous; mid- and hind-leg cartridge buff mixed with tawny olive, and with fuscous on the mid-tarsus. Pectus and venter cartridge buff mixed with tawny olive. Fore-wing with basal third tawny olive, edged proximally and distally with white and with some white admixture along the costa, the distal edge deeply bowed (concavity basad) and passing through the origin of vein *R*1 to the inner margin at one-half; a large semicircular tawny olive patch, resting on the proximal one-third of the inner margin, its curved upper edge reaching to vein *Cu*2, and ringed, except on the inner margin, with white; a large patch of tawny olive on the apical one-third of the wing, ringed with white, its proximal edge roughly semicircular and reaching to the origin of vein *R*5 and down to vein *Cu*1, which it follows for a short distance; these three patches are separated by a medial fascia of fuscous, which sends out a spur to the termen, separating the two distal patches; fringe greyish olive mixed with fuscous. Hind-wing and fringe cartridge buff. Underside of fore-wing cartridge buff, with some scattered tawny-olive hair-scales along the costa, in the discocellular area and in the apical area; fringe bistre, lighter at its base. Underside of hind-wing and fringe cartridge buff.

♂. Resembles the ♀, but the apical patch on the fore-wing has an indentation on its proximal margin.

Expanse : ♂ 28 mm., ♀ 34 mm.

1 ♀ (holotype), Upper Lowa Valley, near Masisi, W. Kivu, 5000–6000 ft., forest and long grass, wet season, February 1924, *T. A. Barns* (ex Joicey collection). 1 ♂ (allotype), Wassaw district, 45 miles inland from Sekondi, Gold Coast (Tring Museum collection).

Nearest to *Dasychira plagiata*, Wlkr. (1855), but probably not a local race, as T. A. Barns took both species in the Upper Lowa Valley. *Aroa perfida*, B.-Bak., Ann. Mag. Nat. Hist. (8) **7**: 546 (1911), and *Dasychira fuscoplagiata*, Auriv. (1925) Ergeb. 2. deuts. Zent.-Afr. Exp. 18 : 1281, are probably synonyms of *D. plagiata*, Wlkr., but in the absence of adequate material in the B.M. collection it has not been possible to confirm this.

Dasychira georgiana incristata, subsp. nov.

(Plate XII, fig. 18.)

♂. Palpus cartridge buff. Antennal shaft white, pectinations honey yellow. Head and thorax whitish, the latter with a central patch of pale yellow orange. Abdomen dorsally antimony yellow mixed with whitish; basal segments, anal tuft and sides whitish. Legs, pectus and venter whitish, fore- and middle-legs marked at regular intervals on the outer side with fuscous black. Wings as in *D. georgiana georgiana*, Fawc. (1901), excepting that the preterminal fascia on the fore-wing, distinct in *D. g. georgiana*, is obsolescent in the present insect. The fuscous shading on the inner marginal area of the hind-wing is only faintly indicated.

♀. Resembles the ♂. The preterminal fascia on the fore-wing is more strongly marked than in the ♂, and is almost straight, not crenate as in *D. g. georgiana*.

Expanse : ♂♂ 34–38 mm., ♀♀ 62–64 mm.

1 ♂ (holotype) and 1 ♂ (paratype), Asuchari, Akusi, Gold Coast, 19–22.xi.1913, *J. D. G. Saunders* ; 1 ♀ (allotype), 2 ♂♂ and 1 ♀ (paratypes), Bibianaha, 70 miles N.W. of Dimkwa, 700 ft., Nov. 1909 and 1910 and Jan. 1912, *H. G. F. Spurrell* ; 1 ♂ (paratype), Kano, N. Nigeria, *F. G. Browne.*

In the British Museum collection *D. g. georgiana* is represented from Natal, Transvaal, Nyasaland, N.W. Rhodesia, Belgian Congo (Lake Kivu) and Uganda. The insect described above appears to be a geographical race, and can be easily distinguished in both sexes by the absence of the black dorsal tufts to the abdomen. A ♀, which very closely resembles the Gold Coast ♀♀, was taken at Nole Kaba, Abyssinia, on 2.v.1926, by Mons. H. Ungemach.

Dasychira chalcocrata, sp. nov.

(Plate XIII, fig. 8.)

♂. Palpus tawny olive, upperside bistre. Antenna tawny olive. Head and thorax tawny olive mixed with fuscous and light elm green, fuscous predominating on the patagium, light elm green on the tegula and at the posterior end of the thorax. Abdomen tawny olive mixed with fuscous, basal segments with a bushy dorsal crest composed of spatulate hair-scales tipped with fuscous. Legs tawny olive mixed with fuscous and light elm green. Pectus and venter tawny olive. Fore-wing with ground-colour light elm green; a light patch at the base of inner margin; fuscous hair-scales scattered irregularly over the wing, especially in the antemedial area; medially an area of vinaceous tawny, having its upper edge on vein *M*1, skirting the reniform and rising to the centre of the cell, its lower edge on the anal vein, its proximal and distal edges reaching the antemedial and postmedial, which are faintly visible in fuscous; some whitish markings between veins *R*4, *R*5 and *M*1, and a few whitish hair-scales on the proximal side of the reniform; preterminal area mainly vinaceous tawny; a fuscous preterminal fascia, parallel with the termen and broken at the veins, which in this area are defined with fuscous; fringe pinkish buff to vinaceous tawny, with interneural fuscous markings which are continued round the apex and along the costa to the postmedial fascia. Hind-wing pinkish buff irrorated lightly with fuscous, more heavily on the costa and discocellulars; fringe pinkish buff, marked at the apex with fuscous. Underside of both wings pinkish buff; fore-wing with discal area irrorated with fuscous and with a fuscous postmedial fascia which ceases at vein *Cu*2; hind-wing with a fuscous spot on the discocellulars and a faint postmedial fascia from costa to vein *M*1; fringes pinkish buff, marked interneurally on the fore-wing with fuscous.

Expanse: 32 mm.

1 ♂ (holotype), Mahatsinjo, near Tananarive, Madagascar (ex Joicey collection).

May be placed near to *Dasychira miselioides*, Kenr. (1914).

Dasychira crecadia, sp. nov.
(Plate XIII, fig. 12.)

♂. Palpus light pinkish cinnamon mixed with bistre and Japan rose. Antennal shaft Japan rose, pectinations drab. Head pinkish buff, the eye surrounded with Japan rose mixed with bistre. Thorax testaceous mixed with drab, cartridge buff at the base of patagium and tegula. Abdomen light pinkish cinnamon. Legs Japan rose to light pinkish cinnamon, fore- and mid-tibiae and tarsi streaked and banded with cartridge buff. Pectus and venter light pinkish cinnamon. Fore-wing varicolorous; the whole wing sparsely irrorated with fuscous black, the costa to the apex edged with Japan rose; basal area mainly Japan rose, followed by a broad band of dark bluish glaucous; this band is followed by a sinuate antemedial fascia of fuscous-black irroration on a ground of Japan rose and light pinkish cinnamon; a ring of fuscous-black irroration enclosing the discocellulars; a postmedial fascia, of similar appearance to the antemedial, curving round the discocellulars and reaching the inner margin at just beyond the middle; between the two fasciae are some patches of dark bluish glaucous; distal third of wing olive grey tinged with dark bluish glaucous and covered irregularly with patches of fuscous-black irroration subterminally; fringe light pinkish cinnamon mixed with fuscous black. Hind-wing and fringe light pinkish cinnamon. Underside of both wings light pinkish cinnamon, darkening to Japan rose in the costal areas; fringes light pinkish cinnamon, tipped in the fore-wing with fuscous black.

Expanse: 39 mm.

1 ♂ (holotype), Upper Lowa Valley, near Masisi, W. Kivu, 5000–6000 ft., forest and long grass, wet season, February 1924, *T. A. Barns* (ex Joicey collection).

Dasychira aeana, sp. nov.
(Plate XIII, fig. 16.)

♀. Palpus, head and antenna drab, the shaft irrorated with fuscous. Thorax drab mixed with fuscous, and an indistinct band of fuscous across the patagium. Abdomen clay colour, with a fuscous-black dorsal crest on each segment. Legs drab mixed with fuscous. Pectus drab. Venter drab to clay colour. Fore-wing cartridge buff mixed with clay colour and irrorated throughout with fuscous, giving a " brown " effect; some irregular longitudinal fuscous markings at the base of the cell; a broad medial band, darker at the edges, caused by an increase in the fuscous scaling, its proximal margin commencing on the costa at one-third and bowed (concavity basad) to the inner margin at one-fourth, its distal margin from the costa at two-thirds and bowed (concavity terminad) to the lower angle of the cell, thence crenate to the middle of the anal vein and outwardly oblique to the inner margin at two-thirds; there is an indistinct patch of fuscous on the costa at four-fifths, and a faintly visible series of small subterminal patches placed interneurally; fringe drab. Hind-wing light drab; an indistinct drab subterminal fascia and a narrow line of drab along the termen; fringe light drab mixed with drab. Underside of both wings, and fringes, cartridge buff suffused with drab; an indistinct drab postmedial fascia across both wings.

Expanse : ♀♀ 39 mm.

1 ♀ (holotype) and 1 ♀ (paratype), Kashitu, N.W. Rhodesia, July and August 1915, *H. C. Dollman.*

Dasychira dollmani, sp. nov.

(Plate XIII, fig. 17.)

♂. Palpus tawny olive, on the outer side bistre. Antennal shaft cartridge buff mixed with Saccardo's umber; pectinations wood brown. Head beneath and round the eye tawny olive mixed with bistre; frons to occiput cartridge buff. Thorax cartridge buff, tegula fuscous mixed with whitish. Abdomen cartridge buff, and a dorsal crest of fuscous black. Fore-leg bistre, ringed with tawny olive and tipped with whitish; middle-leg tawny olive; hind-leg cartridge buff to pinkish buff, the tarsus darker, and a few fuscous scales on the tibia. Pectus and venter cartridge buff, the pectus in front streaked with bistre. Fore-wing of various shades of brown, in which bistre and fuscous predominate; a small patch of cartridge buff at the base of the inner margin; between the upper margin of the cell and the costa an area of argus brown mixed slightly with fuscous, produced to enclose the discocellulars where it is edged with fuscous, and ceasing at the postmedial area; a large and conspicuous whitish patch, mixed with fuscous and argus brown, stretching from the costa before the apex, with two pointed lobes directed terminad, its lower edge bounded by a fuscous streak which follows the proximal half of vein $M3$, its proximal edge bounded by the fuscous postmedial fascia from costa to lower angle of cell, below which the fascia does not extend; there are fuscous markings stretching from postmedial to preterminal areas, between veins $R5$ and $M2$, and also in the neighbourhood of vein $Cu2$; fringe bistre, lighter opposite the veins, and mixed with whitish at the apex. Hind-wing cartridge buff, shaded with tawny olive and fuscous along the termen, more heavily at apex and anal angle; fringe cartridge buff mixed with fuscous. Underside of fore-wing cartridge buff, shaded with fuscous in the cell, costal and apical areas, the discocellulars ringed with fuscous, and a fuscous mark from the costa at three-quarters to vein $R5$; fringe fuscous, mixed with cartridge buff at the vein-ends. Underside of hind-wing and fringe cartridge buff, faintly marked with fuscous in the apical area.

♀. Resembles the ♂, but the whitish subapical patch on the fore-wing contrasting less strongly with the rest of the wing, the upperside of hind-wing and the underside of both wings shaded throughout with fuscous; on the underside of hind-wing there is a darker fuscous spot on the discocellulars, and faintly marked postmedial and subterminal fasciae.

Expanse : ♂♂ 30 and 31 mm., ♀♀ 35 and 36 mm.

1 ♂ (holotype), 5.vii.1917, 1 ♀ (allotype), 26.vi.1915, 1 ♂ and 1 ♀ (paratypes), 8 and 6.vii.1915, Kashitu, N.W. Rhodesia, *H. C. Dollman.*

Dasychira astraphaea, sp. nov.

(Plate XIII, fig. 6.)

♀. Palpus sayal brown, the third segment lighter. Antennal shaft sayal brown, pectinations snuff brown. Head snuff brown mixed with cartridge buff. Thorax snuff brown mixed with bistre, the patagium tipped with cartridge buff. Abdomen snuff brown mixed with bistre and cartridge buff. Legs sayal brown, fore-leg mixed with bistre and with cartridge buff at the end of each tarsal segment. Pectus and abdomen sayal brown mixed with cartridge buff. Fore-wing sayal brown mixed with Prout's brown, giving a snuff brown appearance; a conspicuous white line, running from the base of the wing, along the lower margin of the cell to its end, then along vein *M*3 to the postmedial fascia which it follows to vein *M*2, thence broadly to the apex; the anal vein faintly defined with whitish; a whitish subbasal fascia outwardly oblique from the lower margin of the cell to the anal vein; a whitish antemedial fascia, angled (point inwards) above the cell, again angled (point inwards at the centre of the cell) to a point below the origin of vein *Cu*2, thence oblique inwardly to the anal vein; veins *M*2 and *M*1 defined with white from the cell to the postmedial fascia; a whitish postmedial fascia, oblique outwardly to the junction of vein *M*1 with the longitudinal white line, then oblique inwardly to a point midway between *Cu*2 and the anal vein, thence waved to the inner margin at three-quarters; a whitish subterminal fascia, roughly parallel with the termen, from vein *M*3 to the anal vein; a series of faint dark interneural preterminal spots, edged distally with sayal brown; fringe fuscous, lighter at the vein-ends. Hind-wing and fringe hair brown mixed with drab, the fringe with a lighter line at its base. Underside of both wings snuff brown mixed with pinkish buff; on the hind-wing an indistinct darker discocellular mark and postmedial fascia; fringe of fore-wing fuscous, lighter at the vein-ends, fringe of hind-wing snuff brown mixed with pinkish buff.

Expanse: ♀♀ 34–37 mm.

1 ♀ (holotype) and 1 ♀ (paratype), Bibianaha, Gold Coast, 700 ft., February 1912, *H. G. F. Spurrell*; 1 ♀, Bitje, Ja River, Cameroons, 2000 ft., October–November 1912.

Dasychira ilesha, sp. nov.

(Plate XIII, fig. 7.)

♂. Palpus bistre mixed with cinnamon buff. Antennal shaft pinkish buff at base and at tip, the remainder bistre; pectinations fuscous. Head snuff brown mixed with cinnamon buff. Thorax snuff brown, mixed centrally with fuscous; patagium with a fuscous band posteriorly and tipped with pale pinkish buff; tegula ochraceous orange, and a tuft of the same colour at the posterior end of thorax. Abdomen snuff brown, each segment edged posteriorly with fuscous. Legs, pectus and venter pinkish buff to cinnamon buff, mixed sparsely with fuscous. Fore-wing snuff brown, mixed with bistre and fuscous over almost the whole area of the wing; at the base of the inner margin a large patch of pinkish buff centred with ochraceous orange; below the centre of the cell, situated just above the anal vein, a small circular spot of pinkish buff mixed with ochraceous orange; a bistre antemedial fascia, crenate and indistinct; a line of bistre on each side of the discocellulars; beyond the discocellulars a large snuff brown patch which reaches the costa; a bistre postmedial fascia, crenate, points on the veins, the concavities terminad and filled in with snuff brown, bowed (concavity basad) to vein *Cu*1, inwardly oblique to the anal vein and thence turning outwardly to the inner margin; beyond the postmedial fascia a broad band of bistre running across the wing parallel with the fascia; a large circular subterminal spot, stretching from vein *Cu*2 to the anal vein, pinkish buff mixed with capucine yellow; a similar but more elongate spot at the apex, reaching from vein *R*5 to the costa and termen, its lower margin joined to a small spot between veins *R*5 and *M*1; a series of fuscous interneural preterminal markings, followed by a fuscous line along the termen, the same colour running inwards for a short distance along the veins; fringe fuscous, snuff brown at the vein-ends. Hind-wing pinkish buff mixed with fuscous; fringe pinkish buff. Underside of fore-wing pinkish buff mixed with fuscous, the fuscous admixture being almost absent between the postmedial fascia and the termen, also between the cell, vein *Cu*2 and the inner margin; a fuscous mark on the discocellulars, and a fuscous postmedial fascia roughly parallel with the termen; fringe fuscous, pinkish buff at the vein-ends. Underside of hind-wing pinkish buff lightly mixed with fuscous; a fuscous mark on the discocellulars; a faint fuscous postmedial fascia, roughly parallel with the termen; three large fuscous subterminal spots, one between veins *Sc* and *Rs*, another between *M*1 and *M*2, and another immediately below *Cu*2; fringe pinkish buff.

Expanse: 32 mm.

1 ♂ (holotype), Ilesha, S. Nigeria, *L. E. H. Humfrey.*

Euproctidion, Holl.

Euproctidion, Holl. (1893), Psyche, **6**: 414.

The genus *Euproctidion* was sunk by Swinhoe (Ann. Mag. Nat. Hist. (9) **11**: 401) to *Orgyia,* Ochs., in the Swinhoe sense (i.e. *Dasychira,* Steph., as now treated), Holland's original description being insufficient to show the points of difference. In the genotype, *Euproctidion gabunica,* Holl., of which there is a paratype in the B.M. collection, vein *R*2 in the fore-wing (vein 10 of Hampson's system) rises from the stalk of *R*3 and *R*4, its point of origin being about midway between the apex and the end of the areole.

Euproctidion rhodoides, sp. nov.

(Plate XIII, fig. 19.)

♂. Palpus white, marked with mahogany red on the outer side of the second segment, and with bistre beneath; third segment bistre. Antennal shaft white, banded with bistre; pectinations tawny olive. Head white mixed with pinkish buff, marked with bistre at the base of the antenna. Thorax pinkish buff, mixed on the tegula and posteriorly with bistre. Abdomen pinkish buff mixed with mahogany red, the dorsal crest on the basal segments and the anal tuft tipped with bistre. Fore- and mid-legs with tarsi whitish, lightly mixed with bistre, the hair-scales not raised; the remainder covered with long tufted hair-scales, cartridge buff to pinkish buff, mixed with bistre; some mahogany red on the fore-coxa and at the junction of femora and tibiae of both legs. Hind-leg with hair-scales less tufted, the tarsus bistre mixed with cartridge buff, remainder of leg cartridge buff to pinkish buff. Pectus pinkish buff mixed with bistre, venter pinkish buff mixed with darker shades. Fore-wing etruscan red, shading towards the costa to mahogany red; a prominent whitish marking, edged and mixed with serpentine green, roughly encircling the basal half of the wing with the exception of the costa, the subbasal portion branching into two between the inner margin and the cell, the medial portion a broad band which is widest at the costa, the lower angle of the cell and the inner margin; on the discocellulars a patch of cinnamon buff crossed by a line of serpentine green, and a patch of bistre surrounding the lower angle of the cell; on the distal half of the wing a dappling of small bistre spots placed interneurally over the whole area, and a series of light-coloured spots on the costa; between veins *R*3 and *R*5 a preterminal whitish spot, mixed with bistre; fringe orange vinaceous mixed with pinkish buff, whitish at the vein-ends, and tipped with bistre. Hind-wing white; a narrow band of orange vinaceous along the termen, the same colour running for a short distance into the wing along the veins; fringe whitish. Underside of fore-wing with the whole of the cell bistre and a whitish rounded patch on the discocellulars; area below the cell whitish, grading to orange vinaceous in the distal third of the wing and to etruscan red along costa and termen; a series of whitish spots along the distal half of the costa and a larger one at the apex; fringe orange vinaceous tipped with bistre, interrupted with white at the ends of the radial and medial veins, and with a whitish line along its base. Underside of hind-wing white, with some bistre and orange vinaceous irroration in the costal area and narrowly along the upper part of the termen; fringe whitish.

♀. Closely resembles the ♂, but in the distal half of the fore-wing the bistre interneural spots are obsolescent, and in the hind-wing the whole area is tinged with orange vinaceous. On the underside of the fore-wing the area below the cell is whitish mixed with orange vinaceous.

Expanse: ♂ 26 mm., ♀♀ 33–34 mm.

1 ♂ (holotype), 8.ii.1918; 1 ♀ (allotype) and 1 ♀ (paratype), November 1917; all Solwezi, N.W. Rhodesia, *H. C. Dollman.*

Euproctidion rhodobaphes, sp. nov.

(Plate XIII, fig. 18.)

♂. Palpus and head verona brown mixed with pale pinkish buff. There is a short vestigial proboscis. Antennal shaft pale pinkish buff irrorated with mikado brown, pectinations tawny olive. Thorax verona brown mixed with pale pinkish buff, becoming lighter posteriorly, where the hair-scales are tipped with fuscous; posteriorly in the tegula are a few hair-scales of congo pink, tipped with a darker shade. Abdomen verona brown mixed with pale pinkish buff and posteriorly with fuscous; prominent dorsal tufts on the basal segments, congo pink tipped with fuscous; anal tuft congo pink tipped with fuscous. Fore-leg with tarsus pale pinkish buff, remainder covered with long tufted hair-scales, verona brown mixed with fuscous and pale pinkish buff, and tinged with congo pink. Middle-leg similar, but with shorter hair-scales. Hind-leg not tufted, pale pinkish buff tinged with congo pink, and with two pairs of spurs on the tibia. Pectus and venter verona brown mixed with pale pinkish buff and fuscous. Fore-wing pale pinkish buff mixed with fawn colour and verona brown; a small patch of congo pink at the base of the inner margin; a faint pale pinkish-buff antemedial fascia, outwardly oblique to the lower margin of the cell, thence inwardly oblique to the inner margin at one-fourth; a postmedial fascia of fuscous and pale pinkish buff, commencing from the costa above the distal end of the areole, outwardly oblique to vein *M*2 at one-half, thence almost straight and inwardly oblique to the inner margin at two-fifths; at the angle of veins *M*2, *M*3 and *Cu*1 a small patch of courge green; beyond the postmedial the space between veins *M*2 and *M*3 is filled in with fuscous and pale pinkish buff; between the postmedial and the termen the area is dappled with indistinct dark spots placed interneurally, and a series of light-coloured spots on the costa; a preterminal series of interneural fuscous spots, edged proximally with pale pinkish buff; fringe fawn colour tipped with fuscous, continuing for a short distance beyond the end of the tornus and then abruptly ceasing, which gives the appearance of a projection on the margin, similar to that in *Euproctidion gabunica*, Holl. (1893). Hind-wing congo pink, with some fuscous shading terminally; fringe pale pinkish buff, mixed at the base with fuscous. Underside of fore-wing pale pinkish buff tinged with congo pink; some fuscous shading in the cell and apical area; a series of pale pinkish-buff spots along the distal half of the costa; a dentate preterminal fascia, points on the termen at the vein-ends, from apex to vein *Cu*1; fringe fuscous, pale pinkish buff at vein-ends. Underside of hind-wing pale pinkish buff tinged with congo pink; some fuscous shading in the costal area; fringe pale pinkish buff to congo pink.

♀. Resembles the ♂ in markings, but duller and more uniform in coloration; the dappling between postmedial and termen is obsolescent, and there is no fuscous shading on the upperside of hind-wing and on underside of both wings.

Expanse : ♂♂ 29–32 mm., ♀♀ 38–39 mm.

1 ♂ (holotype), Solwezi, 7.iv.1918 ; 1 ♀ (allotype), Chisanga, 22.v.1915 ; 2 ♂♂ (paratypes), Kashitu, 30.iv.1915 and 27.v.1915 ; all N.W. Rhodesia, *H. C. Dollman.* Also 1 ♀ (paratype), Mlanje, Nyasaland, 7.vi.1913, *S. A. Neave.*

Euproctidion conradti, sp. nov.

(Plate XII, fig. 5.)

♀. Palpus and head dark olive buff, the palpus lighter beneath and tinged with sayal brown. Antennal shaft cartridge buff, pectinations sayal brown. Thorax dark olive buff mixed with sayal brown, the hair-scales posteriorly produced into a tuft. Abdomen pinkish buff ; a sayal brown dorsal crest on the basal segments ; anal extremity tipped with sayal brown. Fore- and middle-legs pinkish buff mixed with sayal brown and dark olive buff, fringed with bushy hair-scales in which the sayal brown predominates. Hind-leg pinkish buff, without fringes. Pectus and abdomen pinkish buff mixed with sayal brown. Fore-wing dark olive buff ; an indistinct darker mark on the discocellulars ; postmedial fascia deep olive edged proximally with pale olive buff, oblique outwardly from the costa at three-fifths to vein *M2* at one-half, crenate inwardly to vein *Cu1* which it follows for a short distance towards the cell, and again oblique inwardly to the inner margin at three-fifths ; costal margin edged with sayal brown, and with a series of cartridge-buff spots between the postmedial and the apex ; at the apex a small almost rectangular patch of cartridge buff ; a preterminal series of interneural triangular deep olive spots ; fringe dark olive buff tipped with deep olive near the tornus, and continuing for a short distance beyond the tornus and then abruptly ceasing, which gives the appearance of a projection on the margin. Hind-wing and fringe pinkish buff. Underside of fore-wing pinkish buff ; apical area lightly shaded with sayal brown ; a series of interneural triangular cartridge-buff spots along the termen, becoming obsolete towards the tornus ; fringe pinkish buff mixed with sayal brown and tipped with deep olive towards the tornus. Underside of hind-wing pinkish buff, with faint postmedial and subterminal fasciae of sayal brown, obsolescent below vein *M2* ; fringe pinkish buff.

Expanse : ♀♀ 34 and 37 mm.

1 ♀ (holotype), Johann-Albrechts Höhe, Cameroons, *L. Conradt,* 1898 (ex Oberthür collection) ; 1 ♀ (paratype), Bitje, Ja River, Cameroons, 2000 ft., October–November 1912 (ex Joicey collection).

Euproctidion striata, sp. nov.

(Plate XIII, figs. 13 and 20.)

♂. Palpus dull citrine mixed with cartridge buff, the third segment tawny olive. Antennal shaft cartridge buff mixed with wood brown, pectinations wood brown. Head and thorax cartridge buff mixed with dull citrine and tawny olive. Abdomen cartridge buff, the segments shaded distally with pale pinkish buff ; small dorsal tufts of russet on the basal segments ; anal tuft tawny olive. Legs imperfect in the type, but apparently cartridge buff mixed with tawny olive and Saccardo's umber. Pectus Saccardo's umber mixed with cartridge buff. Venter mainly cartridge buff, mixed with tawny olive and Saccardo's umber. Fore-wing vari-colorous ; below the cell, and along the inner margin from the base to two-fifths, a whitish patch mixed with dull citrine, with some fuscous irroration ; the cell filled in with fuscous mixed with russet ; on the discocellulars a crescent of cartridge buff, mixed with light orange yellow, with horns directed outwards and between them a spot having the same colours, on a ground of dull citrine; costal area above the cell, and broadly to the apex, dull citrine, with some whitish spots along the costa, two of which are produced downwards on each side of the upper angle of the cell; distal half of wing in several shades of brown, dappled with whitish and ochraceous-orange spots, particularly between lower angle of cell and tornus, each vein bordered above and below by a line of fuscous; a crenate whitish preterminal fascia, points on the veins, enlarged between the apex and vein *R*5 into a patch of whitish; terminal area dull citrine; fringe snuff brown, at the vein-ends whitish. Hind-wing whitish, with a narrow line of russet along the termen; fringe cartridge buff. Underside of fore-wing fuscous, the area below the cell and vein *M*3 whitish; a large whitish spot on the discocellulars; a series of whitish spots on the distal half of the costa; a preterminal whitish fascia composed of subtriangular spots from apex to vein *M*3; fringe snuff brown, at the vein-ends whitish. Underside of hind-wing whitish, with some fuscous markings above the cell and vein *M*2; a narrow line of russet along the termen; fringe cartridge buff, marked at the apex with russet.

♀. A ♀ which appears to belong to this species has a dappling of indian red to coral red spots over the whole of upperside of fore-wing interneurally; the fuscous border above and below each vein is absent, and the whole wing has a darker appearance. The upperside of hind-wing is slightly tinged with orange vinaceous with a line of the same colour along the termen and basal half of the fringe.

Expanse: ♂ 30 mm., ♀♀ 33–35 mm.

1 ♂ (holotype), Mlanje, Nyasaland, June 1925, *H. Barlow* (ex Joicey collection); 1 ♀ (allotype), Solwezi, N.W. Rhodesia, 5.iii.1918, *H. C. Dollman*; 1 ♀ (paratype), Region de M'Pala, Tanganyika, *R. P. Guillemé* (ex Oberthür collection).

Barlowia pyrilampes, sp. nov.

(Plate XIII, fig. 10.)

♂. Palpus orange rufous, distally fuscous black. Antennal shaft fuscous black, pectinations bone brown. Head and thorax orange rufous, the patagium tipped with fuscous black, the tegula mixed with fuscous black. Abdomen orange rufous; a series of fuscous-black dots dorsally; anal tuft fuscous black. Legs orange rufous, mixed with fuscous black, the tarsi entirely fuscous black. Pectus and venter orange rufous, the venter medially with a broad longitudinal stripe of fuscous black. Fore-wing with proximal half orange rufous, distal half fuscous, the veins over the whole wing, and the costa, defined with a darker shade of fuscous; the division between the orange rufous and fuscous areas runs from the costa at one-half, deeply bowed across the cell (concavity basad), thence to the inner margin at three-quarters, a tongue of fuscous invading the orange rufous between the anal fold and the anal vein; there is also a small patch of fuscous medially on the lower margin of the cell; fringe fuscous. Hind-wing orange rufous, with a band of fuscous about 2·5 mm. broad along the termen; fringe fuscous. Underside of both wings, and fringes, as on upperside, but on the fore-wing there is no tongue of fuscous invading the orange rufous between the anal fold and the anal vein.

Expanse: 41 mm.

1 ♂ (holotype), Solwezi, N.W. Rhodesia, 24.xii.1917, *H. C. Dollman*.

The ♀ from Kashitu, N.W. Rhodesia, mentioned in the description of *Barlowia zelotes*, Talbot (1929), with narrow bands and fore-wing measuring 28 mm., is probably the ♀ of the present species.

The ♂ of this species resembles an unnamed species of *Staphylinochrous* (Zygaenidae) in the B.M. collection, from Solwezi.

Aclonophlebia poecilanthes, sp. nov.

(Plate XIII, fig. 9.)

♂. Palpus and antenna fuscous. Head fuscous, with a streak of orange buff commencing at the base of the antenna and running down behind the eye. Thorax fuscous, becoming lighter posteriorly, and mixed on the tegula with orange buff. Abdomen cartridge buff mixed with orange buff, anal tuft fuscous dorsally, orange buff laterally. Legs fuscous, ringed and streaked with orange buff. Pectus fuscous; venter fuscous mixed with orange buff. Fore-wing fuscous; veins defined with pale yellow orange; a large whitish patch on the inner margin, extending from the antemedial to the postmedial area, bounded above by vein *Cu*2, and extending antemedially to the upper margin of the cell; within the whitish patch are four fuscous spots; a pale yellow-orange crescent on the discocellulars; a large whitish patch midway between apex and discocellulars, reaching from the costa to vein *M*2, its proximal margin deeply bowed (concavity basad), its distal margin bluntly angled; a series of whitish interneural postmedial spots joining the last-mentioned patch and the large patch on the inner margin; a series of whitish interneural subterminal spots, the largest between veins *R*4 and *R*5, *M*1 and *M*2, *M*2 and *M*3, and *Cu*2 and the anal vein, the last mentioned being prolonged to the tornus; there is also a spot at the apex; these spots vary in number and size in the paratypes; fringe fuscous, vein-ends pale yellow orange, the latter colour extending for a short distance on to the wing. Hind-wing cartridge buff tinged with pale yellow orange; a fuscous crenate subterminal fascia (obsolescent in the paratypes), broadening into a fuscous patch between the costa and vein *R*5; fringe pale yellow orange, marked interneurally with fuscous between veins *R*5 and *Cu*2, these markings being obsolescent in the paratypes. Underside of both wings, and fringes, as on upperside; costal area of hind-wing pale yellow orange, and a patch of fuscous medially in the same area.

♀. Resembles the ♂, but in the fore-wing the whitish patch between apex and discocellulars relatively larger. The ground-colour of the hind-wing is pale yellow orange, and the subterminal fascia, between the costa and vein *Cu*2, is developed into a broad band which reaches from the postmedial to the preterminal area.

Expanse: ♂ 34–35 mm., ♀ 46 mm.

1 ♂ (holotype), Upper Oso River, N.W. Kivu, 4000 ft., forest with some grass, wet season, February 1924; 1 ♀ (allotype) and 1 ♂ (paratype), Upper Lowa Valley, near Masisi, W. Kivu, 5000–6000 ft., forest and long grass, February 1924; 1 ♂ (paratype), Congo River below Coquilhatville, May 1920; 1 ♂ (paratype), Bolobo, Congo River, Belgian Congo, May 1920; all *T. A. Barns* (ex Joicey collection). Also, in the Musée du Congo Belge (Tervueren), 2 ♂♂, Eala, 1.ix.1914; and 1 ♀, Congo da Lemba, Belgian Congo, 25.viii.1914; *R. Mayne.*

Resembles *Lymantria carriala*, Swinh. (1903), but differs considerably in the pattern of the fore-wing and in the position of the fascia on the hind-wing. *L. carriala* has only one pair of spurs on the hind tibia and must be transferred to *Aclonophlebia.*

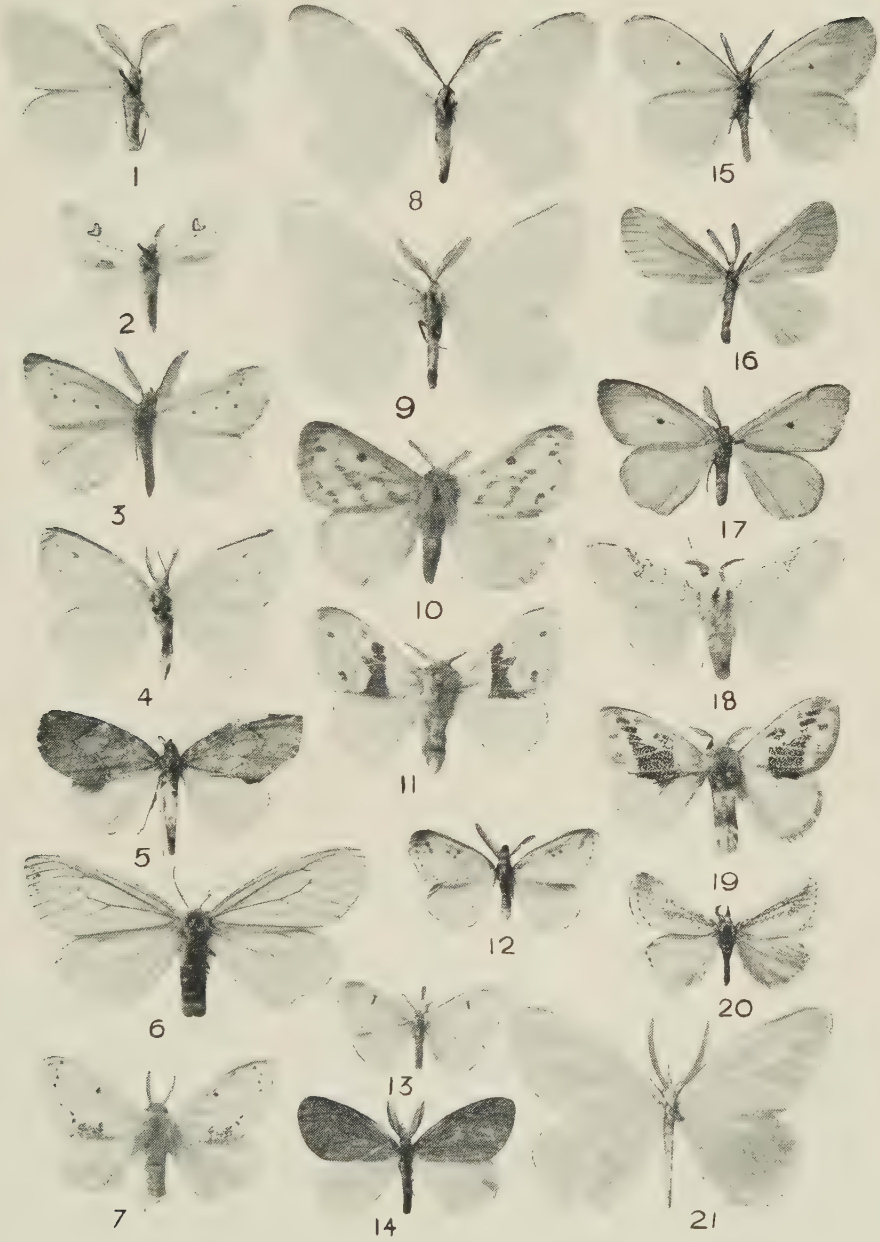
Explanation of Plates XII and XIII.

Plate XII.

Fig. 1. *Redoa mayotta*, sp. nov., holotype ♂ (p. 345).
2. *Naroma nigrolunata*, sp. nov., holotype ♂ (p. 342).
3. *Crorema nigropunctata*, sp. nov., holotype ♂ (p. 344).
4. *Crorema submaculata*, sp. nov., holotype ♂ (p. 343).
5. *Euproctidion conradti*, sp. nov., holotype ♀ (p. 361).
6. *Bazisa phaeophlebia*, Hmpsn., neallotype ♀ (p. 341).
7. *Euproctis hargreavesi*, sp. nov., holotype ♂ (p. 349).
8. *Crorema crocipes*, Boisd., neallotype ♂ (p. 344).
9. *Redoa xanthoma*, sp. nov., holotype ♂ (p. 345).
10. *Euproctis ouria*, sp. nov., holotype ♂ (p. 347).
11. *Euproctis turificator*, sp. nov., holotype ♂ (p. 348).
12. *Euproctis jefferyi*, sp. nov., holotype ♂ (p. 350).
13. *Stilpnotia platyrhabda*, sp. nov., holotype ♂ (p. 341).
14. *Marbla coelebs*, sp. nov., holotype ♂ (p. 352).
15. *Olapa leptomita*, sp. nov., holotype ♂ (p. 346).
16. *Marbla lutulenta*, sp. nov., holotype ♂ (p. 352).
17. *Olapa ituri*, sp. nov., holotype ♂ (p. 346).
18. *Dasychira georgiana incristata*, subsp. nov., holotype ♂ (p. 355 .
19. *Euproctis ceramozona*, sp. nov., holotype ♂ (p. 349).
20. *Lacipa tau*, sp. nov., holotype ♂ (p. 347).
21. *Redoa kenya*, sp. nov., holotype ♂ (p. 345).

Plate XIII.

Fig. 1. *Pirga cryptogena*, sp. nov., holotype ♂ (p. 351).
2. *Dasychira aethalodes*, sp. nov., allotype ♀ (p. 353).
3. *Dasychira aethalodes*, sp. nov., holotype ♂ (p. 353).
4. *Dasychira elaeochroa*, sp. nov., holotype ♂ (p. 354).
5. *Laelia eutricha*, sp. nov., holotype ♂ (p. 352).
6. *Dasychira astraphaea*, sp. nov., holotype ♀ (p. 358).
7. *Dasychira ilesha*, sp. nov., holotype ♂ (p. 358).
8. *Dasychira chalcocrata*, sp. nov., holotype ♂ (p. 355).
9. *Aclonophlebia poecilanthes*, sp. nov., holotype ♂ (p. 363).
10. *Barlowia pyrilampes*, sp. nov., holotype ♂ (p. 362).
11. *Neomardara divergens*, sp. nov., holotype ♂ (p. 350).
12. *Dasychira crecadia*, sp. nov., holotype ♂ (p. 356).
13. *Euproctidion striata*, sp. nov., holotype ♂ (p. 361).
14. *Leucoma brontonepha*, sp. nov., holotype ♂ (p. 342).
15. *Dasychira triselena*, sp. nov., holotype ♀ (p. 354).
16. *Dasychira aeana*, sp. nov., holotype ♀ (p. 356).
17. *Dasychira dollmani*, sp. nov., holotype ♂ (p. 357).
18. *Euproctidion rhodobaphes*, sp. nov., holotype ♂ (p. 360).
19. *Euproctidion rhodoides*, sp. nov., holotype ♂ (p. 359).
20. *Euproctidion striata*, sp. nov., allotype ♀ (p. 361).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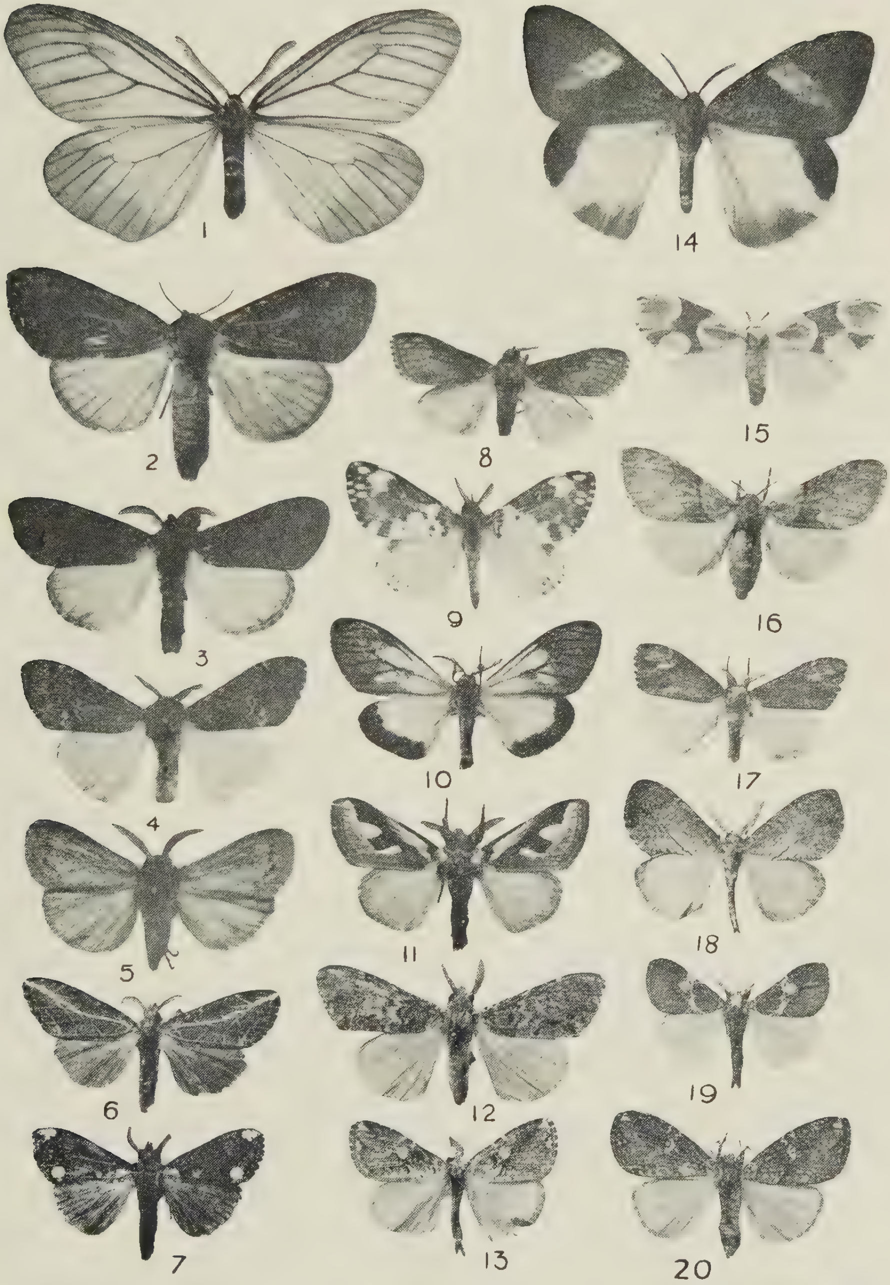
New African LYMANTRIIDAE.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New African Lymantriidae.

DEVELOPMENT OF WINGS IN LEPIDOPTERA

By F. A. Dixey, M.A., M.D., F.R.S.

[Read 4th March, 1931.]

With Nineteen Text-figures.

Our knowledge of the development of the insect wing has been gradually acquired as the result of a long series of investigations. Many writers from the seventeenth century onwards have contributed observations of more or less value to the elucidation of the problem. In the following pages an attempt has been made by means of a study of *Pieris rapae*, Linn., from the last larval stage to that of the perfect insect, to examine, and where possible to verify, the statements of previous investigators; to give reasons for dissenting from conclusions which appear to the writer to be erroneous; and to add a record of certain facts which have not hitherto been recognised, or have been imperfectly understood.

The present inquiry is by no means exhaustive. On several matters our knowledge is still incomplete; for example, the origin, destiny and function of Semper's rods; the part, if any, played by the tracheae in the expansion of the wing after emergence from the pupa; the actual means by which the specialised scent-scales perform their function of disseminating odour. All these and other points await further investigation.

The accompanying figures are not diagrammatic, but in all cases representations, as exact as I could make them, of actual preparations now deposited in the Hope Department of the University Museum, Oxford.

I. Historical.

The existence of wing-rudiments in Lepidopterous larvae was known to Swammerdam, who in 1668 demonstrated their occurrence to the Grand Duke of Tuscany.[1] In 1669 he published his *General History of Insects*, in which he described and figured the wings as they exist in *P. brassicae* under the last larval skin.[2] At about the same time Malpighi, working independently of Swammerdam, recognised the rudimentary wings concealed under the second and third segments of the mature silkworm larva.[3] The same fact was noted by Réaumur,[4]

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[1] 1737, Life by Boerhaave in *Bybel der Natuure*, I, door Jan Swammerdam; Leyden.

[2] 1682, *Histoire Generale des Insectes*, French translation published at Utrecht, pp. 24, 25, Tab. XIII. I have not seen the Dutch original.

[3] "Cùm in Bombyce, ante folliculi texturam, Alarum inchoamenta, sub secundo et tertio annulo latitent."—*Dissertatio Epistolica de Bombyce*, published in London, 1669, with the *imprimatur* of the Royal Society, p. 58. Henneguy (*Les Insectes*, Paris, 1904, p. 9) says that Swammerdam's treatise was published first; but according to Landois (1871, *Z. wiss. Zool.*, **21** : 306) Malpighi's work appeared while Swammerdam's was in the press. The Royal Society's *imprimatur* is dated Feb. 22, 1669.

[4] 1734, *Mémoires pour servir à l'Histoire des Insectes*, Tome I, Paris, pp. 358–59, Pl. 24, fig. 5.

Lyonet,[5] and Hérold.[6] Bonnet[7] and Réaumur followed Swammerdam and Malpighi in holding the "emboîtement" theory. The credit of discerning that the wings are by origin internal and not external belongs to Lyonet.

In 1857 Semper published an important memoir[8] in which he gave the results of his investigation of the condition of the wing in the Lepidopterous pupae of *Saturnia carpini* and *Sphinx pinastri*; one of his figures also represents the developing tracheal system in *Porthesia chrysorrhoea.* He is commendably candid in acknowledging the imperfection of his observations on many points; and it is doubtless due to the fact that his researches did not extend to the early stages, that he speaks of the first stage of wing-formation as the pushing-out (Ausstülpung) of the epidermis in the form of a double layer. In the next stage he describes a membrane enclosing the lumen of the wing; this is the basement membrane of the upper and lower wing-surfaces, which he considers to be constituted by certain formative cells anastomosing by their branches and so forming a network underlying the epidermis, as is well shown in his Pl. XV, fig. 1. The larger tracheal trunks grow from cells arranged in cords which become hollowed out into tubes, the cells not losing their individuality. Within the tubes thus constituted, chitin is deposited in the form of a spiral filament. The finer tracheal branches are developed in single cells. Semper says that he has not been able to observe the first stages in the formation of the ribs (Rippen) or veins (Adern) which constitute the network visible in the wing of the perfect insect. He here speaks of "Rippen" and "Adern" as if they were interchangeable terms. It is evident, however, from his statements elsewhere, that his "Rippe" is an independent structure, though he considers it an antecedent of the "Ader" (vein). The first stage in its development seen by him consists of a tube composed of a single layer of cells and including a fine central fibre, believed by him to be a nerve.[9] These tubes follow the course of the tracheae, which mark out the leading features (Hauptzüge) of the later "ribs" (*i.e.* veins); of the latter there is as yet no trace. In the planned or sketched-out "rib" (*i.e.* vein), one of these tubes is seen in close juxtaposition with each longitudinal branch of a trachea, which is therefore outside, not inside the "rib." The ribs are further developed into a permanent form in which they act as supports to the thin membrane of the wing. Meanwhile the epidermis cells of the wing-surface have become cylindrical, and the scales have begun to grow. These scales arise from large round cells lying between the epidermis and basement membrane, which send up processes between the epidermis cells; each of which processes expands distally into a more or less globular vesicle,[10] the antecedent of the future scale. Semper has not made out whether the large cells detach themselves from the epidermis into the " Hohlraum " between epidermis and basement membrane, or whether they result from a division of the epidermis cells. " Hairs " and scales are essentially the same. A chitinous sheath always results from excretion by an epidermic layer, and acquires its characteristic peculiarity by exposure to the air; pathologically it may arise from certain special cells. As the chitin of the wings gets portioned off, the epidermis cells diminish in size and disappear, leaving no trace. The chitinous envelope grows in all directions, and falls into folds which disappear at emergence. At this stage the " ribs " with included nerve take on a further development, and give rise to the permanent veins. On this point Semper's language is perhaps not quite clear, but he appears to state that the cells of his " wing-ribs " become fused externally with the epithelium of the accompanying trachea; and internally excrete a cuticle which thickens and finally unites with the cuticle of the true epidermis (*i.e.* of the wing-surface), after which the enveloping cells (of the rib) gradually disappear. Following the degeneration of the intermediate cell-layers the two wing-membranes so closely approach one another that the " ribs," previously invisible, come into view and give the wings their characteristic mapping. Semper thus makes the " rib " the antecedent of the " vein "; in this sense he distinguishes the one from the other. He thinks that the cuticle of the scale is continuous with that of the surface of the wings; [11] this thickens on the scale into longitudinal and cross bars; the scale is now ready for pigment. When the scale is finished, the forming cell disappears, and there remains the chitinised scale with its root fixed in a socket of the epidermis. The expansion of the wing takes place by the smoothing out of the folds previously mentioned, this being caused by blood-pressure through the veins from the body-cavity (shown by the fact that cut veins bleed), and by inflation through the tracheae; at the same time the chitin of the wing consolidates. Semper maintains that chitin is an excretion, not a product of cell-fusion. He is certain about his underlying " forming-cells," and insists on the fact that the scales and hairs of insects are not homologous with those of vertebrates. Menzel (1850) and Hollard (1851) tried in vain to establish the contrary; the latter considered that the scales of Lepidoptera are constituted by fine parallel tracheae (*i.e.* the longitudinal bars) between epidermic layers. There is a fundamental distinction between the hairs and scales of insects on the one hand, and appendages such as their wings and legs on the other.

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[5] 1762, *Traité Anatomique de la Chemille qui rouge le Bois de Saule*, La Haye, pp. 449–50.

[6] 1815, *Entwickelungsgeschichte der Schmetterlinge*, Cassel und Marburg, pp. 29–31. Hérold does not allow that Lyonet's observation had reference to the wings:—"Der *Keime der Flügel* gedenkt *Lyonnet* [sic] bey der Raupe von *Phalaena Cossus* L. nicht. . . . Er vermuthet, dass diese Massen die Keime der Künftigen Beine des Schmetterlings wären," p. 30. But Lyonet's own words leave no doubt on the point:—"Ces quatre masses, au premier coup d'oeuil, pourroient aisément être prises pour quelque graisse particulière; mais, les ayant examiné, j'ai trouvé qu'elles avoient toute l'apparence de Corps singuliers, différens des autres parties de l'Animal. . . . Leur nombre et la place qu'elles occupent, donnent lieu de soupçonner qu'elles pourroient bien être les principes des ailes de la Phalène."—*Traité Anatomique*, pp. 449–50. See also *ib.*, pp. 260–61, and Pl. XI, figure at bottom of plate, not numbered, but wrongly said in *Errata* (p. 24) to be Pl. X, fig. 7. The explanation of the figure is given, under its right designation, on pp. 592–93, where the statement "elles pourroient bien être les principes des Ailes de la Phalène" is repeated. It is not easy to see what warrant Hérold could have for his dictum above quoted.

[7] 1781, *Œuvres d'Histoire Naturelle*, Tome VIII. Neuchatel, pp. 300–1, etc.

[8] 1857, *Z. wiss. Zool.*, **8**: 326–39, Pl. XV.

[9] Semper, *loc. cit.*, Pl. XV, fig. 6; partly reproduced by Dr. Sharp, 1901, *Cambridge Natural History*, VI, Insects, Part II, p. 334, fig. 175B.

Semper's account, which only deals with the final stages of wing-growth, is thus good as far as it goes, though omitting many details, and not altogether accurate. Some of his figures have been copied by the authors of text-books, *e.g.* Sharp (1901), Henneguy (1904), Schröder (1912). He gives the first clear description of the growth of scales and hairs. He is also the first to observe the structure known as the " wing-rib," but is mistaken as to its relation to the permanent " vein."

Weismann's investigations in the embryology of Diptera [12] showed the true significance of the larval wing-rudiments noticed by earlier observers. He found that they were of similar constitution to the numerous bodies to which he gave the name of " Imaginalscheiben " (imaginal discs or folds); and though he at first considered these wing-rudiments to be derived from the cellular sheath of tracheae and nerves, he was eventually led by his study of the development of *Corethra* to conclude that they were the result of hypodermic downgrowths.

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[10] Semper, *loc. cit.*, Pl. XV, fig. 2. Reproduced by Dr. Sharp, 1901, *Cambridge Natural History*, VI, Insects, Part II, p. 334, fig. 175A.

[11] See his figure of hairs on the antenna of *Saturnia carpini*, *loc. cit.*, Pl. XV, fig. 3.

[12] 1864, *Z. wiss. Zool.*, **14**; 1866, *ibid.*, **16**.

In 1871 LANDOIS published an account of his researches on the development of the wings in *Vanessa urticae* and *Pieris brassicae*.[13] He found the wing-rudiments already present in larvae 4 mm. long. In larvae after the first moult he observed a group of club-shaped cells at the base of the wing-rudiment, in connection with the sheath of the longitudinal trachea. These he supposed to be derived by modification from the cells of the actual rudiment. Within each of these club-shaped cells was developed after the second moult a tangled tracheal capillary, as previously observed by Semper, with whose figures of these structures Landois's are in agreement.[14] The tracheal " knots " (Knoten) or " balls " (Knäuel) are conjectured by the latter to be formed by a transformation of the nucleus of the mother cell; he states that they are at this stage full of air derived from the tracheal trunk. After the fourth moult the wing-rudiments protrude through the muscular sac (Muskelschlauch); the hypodermis opens, and the wings henceforth appear as projections of the external skeleton. They are, however, not evaginations of the integument, but tracheal structures. The tracheal capillaries now occupy approximately the position of the later-formed veins. After the caterpillar (of *V. urticae*) has hung itself up, the rudiments enlarge by the unrolling of the tracheal bundles and the flow of blood into the wing-sac. If the pupa, immediately it appears, be plunged into water or dilute alcohol, its antennae, proboscis, palpi, wings and legs can be separated from each other. Besides the tracheoles, which so far have provided for respiration in the wing, there now appear the main tracheal trunks and wing-ribs (Semper's ribs). These latter are elastic cords surrounded by a single layer of cells; they take part in the formation of the adjacent ribs (*i.e.* veins). Landois describes them as secreting inwardly a concentrically striped core (Semper's " nerve "). Close to them (dorsally to them in his Fig. 10), main tracheal stems appear, with spiral fibres. The development of these tracheae and ribs gradually replaces the tracheal capillaries. The ribs in the strict sense (*i.e.* Semper's ribs) run in cavities between the wing-surfaces, which now lie close to one another. They thus cause the archings-out of the wing-membrane which are known as " veins." The ribs lie close to the under surface of the wing,[15] and grow with it. Thus the " veins " are not simple structures, but tracheae, " ribs " and arched-out cuticle all take part in them. There is sufficient space within them for the flow of blood. Landois says that his observations on scale-formation do not quite agree with those of Semper; probably because of the different material employed. He thinks that each formative cell sends out a process on either side, uniting with one from each adjacent cell. It is " self-evident " that the wings are not outgrowths of the integument, but tracheal structures. The scales are developed from subhypodermic cells, and cannot be held to be supra-integumental structures in the strictest sense. The longitudinal and cross striae of the scale are due to shrinking; the scale-holder is formed from a hypoderm cell. Entrance of air unfolds the wing; the footstalk of the scale dries up (einschrumpft), and so the scale can be filled with air. Landois's Figs. 1–7 are from *P. brassicae*, Figs. 8–12 from *V. urticae*.

Landois thus confirms Semper's observation of the provisional tracheal

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[13] 1871, *Z. wiss. Zool.*, **21**: 305–16, Pl. XXIII.

[14] Semper, *loc. cit.*, Pl. XV, fig. 7. Landois, *loc. cit.*, Pl. XXIII, fig. 3.

[15] Landois's Fig. 10 shows them close to the *upper* surface (his figure having the dorsal side lowest). They clearly underlie the upper surface in my preparations.

capillaries, though he wrongly supposes them to be derived from the cells of the actual wing-rudiment. He recognises and figures Semper's "ribs," distinguishing them from the finished veins and from the tracheae. He finds the wing-rudiments already present in very young larvae, and, impressed with the absence of stigmata in the 3rd and 4th larval segments, regards the wings as essentially tracheal structures.

In 1875 KÜNCKEL D'HERCULAIS[16] confirmed and extended Weismann's later view as to the hypodermic origin of the imaginal discs.

In 1876 GANIN published researches on postembryonal development in Diptera, Hymenoptera, Lepidoptera and Coleoptera.[17] He recognises the existence and hypodermic origin of Weismann's imaginal discs, but puts limits to the operation of histolysis. (With regard to the alimentary tract, "eine Histolyse in Sinne Weismann's existirt nicht.") He rightly attributes the tracheal system in the imaginal wings and legs not to a development of the tissue of the disc, but to an invasion of the organ by prolongations of the tracheal system from the body-cavity. He appears to think that the envelope of the wing-rudiment has only a provisional significance ("Die Vertiefung sich zu einem Säkchen differenzirt, welches die sich entwickelnde Extremität von aussen einhüllt und nur eine provisorische Bedeutung hat").

Ganin's contribution is superior to Landois's in respect of his recognition of Weismann's imaginal discs, and of his account of the original tracheal supply of the thoracic appendages.

In 1878 DEWITZ[18] published his researches on the development of the thoracic appendages in Ants and Lepidoptera. He found that the general mode of development was the same for both; his examples of Lepidoptera were *Smerinthus ocellatus* and *Pieris brassicae.* He describes and figures the wing-rudiment in a larva of *S. ocellatus* about an inch long, as an ingrowth of the hypoderm forming a pocket, and maintaining its connection with the hypoderm of the body by a hollow footstalk which shows, in the form of a narrow orifice, the original aperture of invagination. At the passage into the pupal stage, observed in *P. brassicae*, the aperture of invagination enlarges and permits the emergence of the wing-rudiment. This grows rapidly; its hypodermic envelope is smoothed out, thickens, and becomes indistinguishable from the neighbouring hypoderm. The thoracic appendages in all orders of insects arise from thickenings of the hypoderm; in those with incomplete metamorphosis, from direct outgrowths; in those with complete metamorphosis, from ingrowths of the hypoderm forming pockets in the interior of the body. Weismann's original view that in the MUSCIDAE the imaginal disc is by its origin in connection with tracheae and nerves, but not with the hypoderm, is erroneous. Tracheae and nerves enter the disc, and this may have given rise to the notion that the new structure is developed entirely from them and has no connection with the hypoderm. Landois is mistaken in thinking the wings purely tracheal structures (his 3rd and 4th segments are Dewitz's 2nd and 3rd, the former counting the head as the 1st); their foundation is laid by the ingrowth of hypoderm. With Ganin's results Dewitz is in general agreement, though he regards the envelope of the limb-rudiment as a permanent, not a provisional feature. A further investigation by Dewitz, published in 1881, on wing-development in PHRYGANIDAE and Lepidoptera,[19] confirmed and elucidated his former results.

[16] 1875–78, *Recherches sur l'Organisation et le développement des Volucelles.* Paris.

[17] Ganin's original memoir is in Russian. A summary appeared in 1877, *Z. wiss. Zool.*, **28.**

[18] 1878, *Z. wiss. Zool.*, **30**, Suppl.

[19] 1881, *Berl. ent. Z.*, **25** : 54–60, Pl. III; Pl. IV, figs. 1, 2.

He finds that in Phryganids, as in Ants, etc., the wings are ingrowths of the "matrix" (*i.e.* the hypoderm). His text and figures show very clearly the folding of the wing-rudiment (including mesodermic tissue), the envelope, and the continuity of envelope with thoracic hypoderm; also the escape of the wing by enlargement of the original invagination cavity. He speaks of a chitinous accompaniment of the invagination, continuous with the external chitin and shed at moults. His figures of Lepidoptera in this communication are of *Deilephila euphorbiae.*

It is thus to Dewitz that we owe the first approximately complete account of wing-development. Confirming Ganin's account of the part played by Weismann's imaginal discs, and of their invasion by tracheal outgrowths, he added thereto a detailed description of the original hypodermic ingrowth; showing its elaboration into a pocket with its included germ and envelope, and rightly asserting, in opposition to Ganin, that the latter is a permanent, not a provisional structure.

In this latter contention he was confirmed by PANCRITIUS, who as a result of his examination of the larval and pupal condition in *Smerinthus populi* clearly recognised, in agreement with Dewitz and against Ganin, that the envelope of the wing-germ (Flügelscheide) becomes, after the extrusion of the wing, a part of the thoracic epithelium.[20] He follows both the latter authorities in their recognition of Weismann's discs, and notes that the lumen formed by the secondary folding of the wing-germ is in communication with the interior of the body-cavity. The coarsely granular cells that he speaks of as investing the tracheal trunk underlying the rudiment, are doubtless the capillary tracheoles in cross section.

The next important contribution to the subject was made by SCHÄFFER.[21] He affirms his almost entire agreement with Pancritius (making no mention of Dewitz), but dissents from many of the statements of the older authorities, Semper and Landois. For the larval condition he used *P. brassicae*, for the pupal *V. urticae*; he agrees with Landois as to the cellular origin of the first capillary tracheoles. Schäffer says that he can positively affirm the derivation of the scale-forming cells from the hypoderm. The "pillars" between the scale-forming cells are epithelial in origin, as are similar structures in other Arthropods. Just before emergence from the pupa, the two wing-surfaces are thrown into folds. The central membrane, which had resulted from the fusion of the two basement-membranes, is reabsorbed; so that at this stage the wing is directly traversed by many slender pillars connecting the two surfaces. The cuticle appears after the establishment of the folds; its occurrence puts a limit to the growth of the wing. It becomes thickened on the surface over the veins,[22] and is here cleft into two longitudinally-striated layers, between which is a cross-striped layer showing cavities (Pl. XXX, fig. 39). In this figure, reproduced by Dr. Sharp,[23] *r* denotes a tube formed within the vein by the remainder of the two ground-membranes; it is traversed by the wing-rib of Semper. With regard to the wing-ribs, Schäffer has been able to observe with certainty the connection (Zusammenhang) of these cellular tubes with the tracheae. This occurs in the base of the wing, where the lumen of the tracheae is greatly widened. In cross section the adult rib presents for the most part a cylindrical tube which is fitted with a very thin chitinous intima that carries delicate aborescent processes (Bäumchen). A flat view of these processes is given by tangential sections (Schäffer, Pl. XXX, fig. 38). Schäffer cannot say whether the twigs anastomose; he thinks they do not. A central rod runs through the rib, which rod in longitudinal section shows a clear longitudinal striation; this according to Semper is a nerve, but Schäffer cannot regard it as anything but an exudation-product of the wall-cells. He could only find ribs in the basal half of the wing; he concludes therefore that they are not elastic, and are drawn out of the distal region at the unfolding of the wing. He finds no confirmation of Semper's view as to the fusion of the chitin of the rib with the outer chitin of the wing. It is remarkable that he has observed no tracheae in the adult wing. The " Zellstränge " observed by Brauer and Redtenbacher[24] are identical with Semper's ribs. These authors corroborate Semper's observation as to the connection of the ribs with the tracheae; they appear, however, to consider the ribs as antecedents of the tracheae, and to agree with Semper's view, no doubt a mistaken one, as to the part taken by ribs and tracheae in the formation of the veins.

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[20] 1884, *Königsberger Dissertation* (Vorläufige Mittheilung in 1884, *Zool. Anz.*, **7** : 370–73).

[21] 1889, *Zool. Jahrb.*, **3** : 637–52, Pl. XXX.

[22] Schäffer describes the thickening as taking place on the *upper* instead of the *under* surface of the wing; this mistake in the text (p. 646) is repeated in his figure (Pl. XXX, fig. 39), copied by Dr. Sharp, *loc. cit.*, p. 330, Fig. 170A. In these figures the underside is represented as uppermost.

[23] 1901, *Cambridge Natural History*, VI, Insects, Part II, p. 330, fig. 170.

It is seen that Schäffer develops Semper's account of his " wing-ribs," but dissents from his view as to the nature of their central cord; nor does he agree as to the fusion of the chitin of the rib with that of the surface of the wing. With regard to the origin of the wing-rudiment, he follows (rightly) the view of Dewitz and Pancritius against that of Landois.

VERSON recognised (1890) the wing-rudiments not only in larvae of the silkworm just emerged from the egg, but even in the egg itself.[25] He appears to identify them with the missing stigmata of the 2nd and 3rd segments. He describes the formation of capillary tracheoles and their relation to the embryonic wing; adding, in agreement with Landois, that the significance of an organ of respiration must be attributed to the wing of the Lepidoptera.

The most detailed account of wing-development in the Lepidoptera hitherto published is that furnished by GONIN in 1894.[26] His investigation, which was conducted on the larva and pupa of *Pieris brassicae*, has been largely adopted as a basis for treatment by subsequent authors, as by Sharp (1901, *Cambridge Natural History*, Insects, Part II), and by Henneguy (1904, *Les Insectes*, Paris). Gonin's observations are in many respects more complete than those of previous authors; and where he differs from his predecessors, his conclusions are generally, but not always, more correct. In the account on a later page of my own investigations, I have stated the points on which I am able to confirm Gonin's work, and also those in which I am constrained to differ from him.

A. G. MAYER in 1896 published good figures of the embryo wing in *P. rapae*.[27] They represent a somewhat later stage than Gonin's figure of *P. brassicae* at the end of the third stage (reproduced by Henneguy, *Les Insectes*, p. 563), but, being taken at the level of the aperture of invagination, they do not, as that figure does, make the envelope continuous all round with the wing-rudiment. Mayer notes that leucocytes are present between the basement-membrane and the hypodermis, and concludes therefore, in agreement with Schäffer, that the former is not absolutely uninterrupted. He gives a good representation of early scale-formation in *V. antiopa*; stating, also in confirmation of Schäffer, that the scale-forming cells are undoubtedly modified hypoderm cells, and representing them as vacuolated.

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[24] 1888, *Zool. Anz.*, **11**: 443–447.

[25] 1890, *Zool. Anz.*, **13**: 45, 116.

[26] " Recherches sur la métamorphose des Lépidoptères," 1894, *Bull. Soc. vaud. Sci. Nat.*, (3), **30**: 89–139, Pls. XI–XV.

[27] " The Development of the Wing Scales and their Pigment in Butterflies and Moths," 1896, *Bull. Mus. Comp. Zool. Harvard*, **29**: 209–36, Pls. 1–7.

Mayer's work is valuable in confirming the results of previous authors as to the hypodermal origin of the wing-germ with its envelope, and the early formation and growth of the scales. His figures, semi-diagrammatic in character, are particularly well executed.

An important paper was published in 1900 by W. F. MERCER.[28] The investigations of which this is a record were undertaken at the suggestion of Professor Comstock, who had found reason for thinking that in some respects the account given by Gonin was inaccurate. As material for his work on wing-development, Mercer, like Mayer, made chief use of *Pieris rapae*; supplementing it at some points with preparations from two moths, viz. *Sanninoidea exitiosa* and *Automeris io*. His main difference from Gonin consists in the view that he takes of the means by which the wing-rudiment becomes external at the end of larval life. This in Gonin's opinion takes place by destruction of the envelope; Mercer, like Dewitz and Pancritius, holds that the wing escapes through the original aperture of invagination; the extremities of the envelope undergoing fusion, as shown in his figures of *Sanninoidea* and *Automeris*, with part of the body hypodermis, any slack that remains going to make up the ventral body-wall. The objects thought by Gonin to be debris of the disintegrated envelope, are particles of coagulated "moulting fluid." The much-discussed "rib" of Semper, figured by Mercer on a large scale in his Plate V, is, according to him, a degenerating trachea. "It is evident," he says, "that this degeneration of the wing-tracheae finally becomes complete; for in the wing-veins of the adult the tracheae are lacking." Reasons for dissenting from this view of the "rib" will be given later.

Mercer in the main confirms Gonin, except with regard to the destiny of the envelope. His identification of Semper's rib with a trachea has been uncritically accepted by later authors.

The scope of the detailed and careful study of the wing-veins of insects published by C. W. WOODWORTH in 1906 does not include any extended account of the development of the wings themselves.[29] He, like Mercer, identifies Semper's rods with tracheae, writing of them as follows: "The problematical 'rods of Semper,' that have been repeatedly described in Lepidoptera, are only imaginal tracheae in the process of development and not essentially different from any other tracheae in insects' wings" (*loc. cit.*, p. 52). No essential relation, according to Woodworth, exists between tracheae and veins (*loc. cit.*, p. 47).

The development of the wings in PHRYGANIDAE had already been shown by Dewitz, as mentioned above, to be essentially the same as in Lepidoptera. In 1913 W. S. MARSHALL published a careful investigation of the process in the Phryganid *Platyphylax designatus*, Walk.[30] He confirms Dewitz's account of the origin of the wings as hypodermic thickenings which invaginate and form a cavity communicating with the exterior by a "peripodial" pore. A secondary cavity, communicating with the body-cavity as in the Lepidoptera, is formed within the wall of the hypodermic invagination, and the fold thus effected, which is the rudimentary wing, becomes pushed out through the peripodial

[28] "The Development of the Wings in the Lepidoptera," 1900, *J. New York Ent. Soc.*, **8**: 1–20, Pls. 1–5.

[29] "The Wing Veins of Insects," 1906, *Tech. Bull. Agric. Exper. Stat. Univ. Calif.* (Ent.), **1**: 1–152.

[30] 1913, *Z. wiss. Zool.*, **105**: 574–97, Pls. XXVII–XXIX.

pore and so becomes external. He has not found anything corresponding to the fusion of the hypodermal layer and the peripodial membrane [31] as described by Mercer, but recognises that the peripodial pore becomes a long narrow slit, and so allows the emergence of the wing-rudiment. Tracheae do not enter the developing wings until the latter have become external.

The essential identity of the process of wing-development in Trichoptera and Lepidoptera, first propounded by Dewitz, has thus been amply confirmed by Marshall.

II. Growth of the Wing-rudiment in *Pieris rapae*, Linn.

(a) *The prepupal stages up to the appearance of the wing as an external structure.*

It has long been well known that each wing of a Lepidopterous insect originates in the young larva by an invagination of the hypoderm (Dewitz, Pancritius, Schäffer). Of the bag or sac thus formed, the upper wall becomes thickened, and eventually constitutes the wing of the adult; the lower wall remains comparatively thin. The upper wall next becomes bent so as to form a loop or sac open towards the body-cavity, which in insects, as is well known, is a haematocele and not a coelom. The outer limb of this secondary loop or sac becomes the upperside of the adult wing; the inner limb becomes the underside. Between the two, blood, capillary tracheae and leucocytes pass from the body-cavity into the wing-rudiment through the open mouth of this secondary loop or sac, thus tending to keep the two wing-surfaces apart. Meanwhile, the thin lower wall of the original invagination has become reflected round the fundus of the secondary sac, accompanying it for some distance along its outer aspect; finally becoming folded outwards upon itself and so resuming its continuity with the general hypoderm. In this way is formed the envelope of the wing-sac; any space that exists between the envelope and the wing-rudiment being a relic of the original invagination-cavity. It needs hardly to be said that this primary cavity of invagination, which opens between the hypoderm and the external integument of the larva, is completely distinct from the secondary cavity of the sac, which communicates with the general body-cavity. In the wing of a larva ready to spin but not yet settled down, the relations of wing-sac, envelope and body-wall, as just described, are clearly visible (Fig. 1).[32]

The successive stages of the growth of the wing up to the time of the last larval moult have been well figured by Gonin,[33] but it should be observed that these figures are not easily intelligible unless it is remarked that they represent sections which are not all taken at the same level. Gonin's Fig. 8A, for instance, shows the envelope of the wing-germ continuous with the general hypodermis; this is described as " Coupe de l'extrémité anterieure." Fig. 8B shows the envelope continuous with the wing-germ itself, and is described as " Coupe au niveau du hile "; the " hilus," of course, being the region where the interior of the rudimentary wing (otherwise the "secondary sac") communicates with the general body-cavity; *not*, as might possibly be supposed, the neck of the original invagination.[34]

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[31] The term " membrane péripodale " was introduced by Van Rees (1888, *Zool. Jahrb., Abt. Anat. Ontog.*, 3) to denote that portion of the hypodermic involution surrounding the leg-germ which corresponds to the envelope of the developing wing. The term peripodal (Mercer) or peripodial (Marshall) has since been applied to the leg-germ and wing-germ indifferently.

[32] The preparations from which were drawn the figures illustrating this paper, were made by my friend Dr. H. Eltringham, F.R.S., to whom I am greatly indebted for his ready and efficient help. They were made in every case from the summer brood of *P. rapae*, Linn.

[33] " Recherches sur la métamorphose des Lépidoptères," 1894, *Bull. Soc. vaud. Sci. Nat.*, (3), **30**: 89–139, Pls. XI–XV.

The wing, having thus begun its existence as an internal structure, becomes external during the last stage of larval growth. According to Gonin, whose view is adopted by Henneguy, this is effected by a destruction of the envelope, which, as we have seen, has hitherto been folded around the wing-rudiment. According to another view the wing becomes external by a process of evagination. Dr. Sharp (*loc. cit.*, p. 329) leaves the question open. I cannot, however, find support for Gonin's view of the destruction of the envelope; nor, on the other hand, can I agree that the rudimentary wing becomes external by a simple turning inside out of the original pocket of invagination.

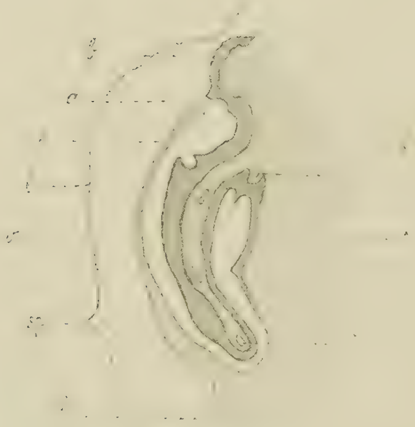

Fig. 1.—Larva ready to spin. × 30. Part of transverse section through thorax, showing developing wing in longitudinal section, still within the larval integument. The wing is seen to be a pushing out of part of the floor of the original invagination into the invagination-cavity; the body-cavity being continuous with the interior of the wing and also with the interior of the loop formed by the wing-envelope.

w, wing; *b*, body-wall of pupa; *e*, wing-envelope; *c*, body-cavity; *a*, aperture of original invagination; *t*, trachea; *l*, larval integument about to be shed; *sp*, spine.

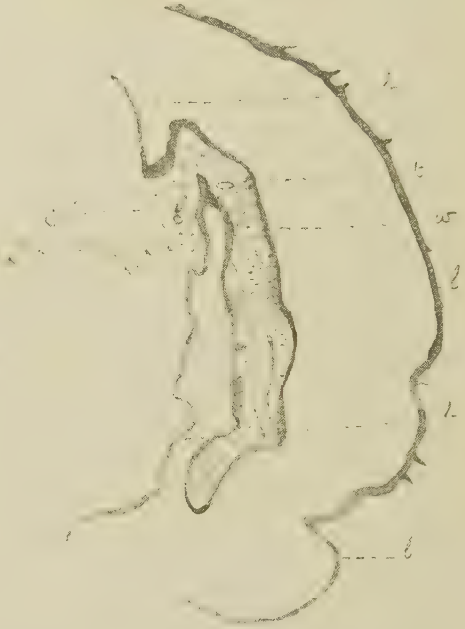

Fig. 2.—Larva 8 hours after formation of girdle. × 30. Part of transverse section of thorax, showing developing wing in longitudinal section, still within the larval integument, but now external to the pupal body in consequence of the unfolding of the loop of the wing-envelope.

w, wing; *b*, body-wall of pupa, constituted in part by the unfolding of the wing-envelope; *c*, body-cavity, continuous with the interior of the wing; *t*, trachea; *l*, larval integument about to be shed.

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[34] Schäffer's Fig. 35 *loc. cit.*, Pl. XXX) is also taken before or behind the level of the aperture of invagination.

It appears to me that what happens is this; the growth of the wing, which is very rapid in the immediately prepupal condition, has the effect of unrolling, as it were, the folded portion of the envelope, and thus straightening it out into line with the general hypoderm of the body-wall ventrally to the original invagination. This necessarily has the effect of enlarging the opening of the invagination cavity; and the wing being thus liberated, becomes external by its own simple growth and consequent extrusion through the mouth of the primary invagination, aided no doubt by fluid pressure from the body-cavity, with which its own cavity remains in communication. The envelope, which has never lost its continuity with the general hypoderm, is drawn to the inner or axillary aspect of the wing and takes its part accordingly as a portion of the ventral body-wall (Fig. 2).

It is not easy to see how a breach could take place in the continuity of the envelope, such as Gonin supposes, without leaving the body-cavity in direct communication with the exterior; nor does there appear to be any provision by which the body-wall, if thus interrupted, could be reconstituted. It must always be borne in mind that wing-rudiment and envelope are continuous in origin, both being modifications of the hypodermic wall of the primary invagination; and in no preparation have I found any indication of that continuity being broken. The successive changes in the relative position of the hypodermic areas corresponding to wing, envelope and body-wall respectively, are more readily comprehended if it be realised that the problem is one of three dimensions; and not merely of two, as shown in sections. The folding of the envelope round the fundus of the wing-rudiment is due to the pushing out of that rudiment into the primary cavity to form the secondary sac; while the subsequent unfolding of the envelope is an accompaniment of the prepupal growth of the wing. From the preceding account it follows, (1) that the space between the wing-rudiment and its envelope is a relic of the original cavity of invagination; while both surfaces, upper and under, of the adult wing represent a part of the original floor of that cavity; (2) that the interior of the wing, and the space included within the outermost loop of the envelope, are diverticula of the general body-cavity.

It has been already noticed (*supra*, p. 372) that Mercer is of opinion that the escape of the wing is effected by the enlargement of the original aperture of invagination (Marshall's "peripodial pore"), through the fusion of the extremities of the envelope with part of the hypodermic layer bounding the body-cavity. Marshall, in Trichoptera, finds no indication of this. Some of Dr. Eltringham's preparations show appearances like those of Mercer's Figs. 19 and 20; but I doubt whether the latter's interpretation of these appearances is correct. It seems to me that they are due to the occasional superposition of the two layers of the fold of the envelope rather than to any actual fusion. It is possible that the slips of muscle figured by Gonin (*loc. cit.*, Pl. XIII, fig. 18) and by Marshall (*loc. cit.*, Pl. XXVIII, figs. 13A, 16A and 18) may assist in unrolling the fold of the envelope, and so in enlarging the aperture of invagination. Dr. Eltringham's preparations show strands of muscle-fibre in a corresponding situation; but it is difficult to see how, having started the process, they could, without finding a fresh *point d'appui*, continue to exercise a straightening pull on the envelope. I have little doubt that the principal function of these muscular strands is to detach the hypodermic layer from the larval cuticle which will be shed at the time of pupation. On the whole then, as already stated, I am inclined to think that the unrolling of the envelope and consequent enlargement of the aperture of invagination is mainly due to the growth of the wing-rudiment aided by fluid pressure passing into its interior, and into that of the envelope, from the body-cavity. These conclusions are in substantial accordance with the views of Dewitz, Pancritius and Marshall; but not with the view of Gonin, followed by Henneguy.[35]

(b) *The later prepupal stages.*

The wing having thus become external, though still concealed within the chitinous integument of the larva, assumes in the course of its growth a twisted and convoluted appearance aptly compared by Gonin to that of the convolutions of the mammalian cerebral cortex. At a somewhat later stage, when the rapid growth of the wing within a limited space results in its being thrown into deeper folds, the clefts which cause the convoluted appearance of the larval wing become still more fully established. The consequent ridges and furrows seen in section necessarily affect both the upper and under surface of the wing; but until a series of sections is examined, it may seem that one surface is more deeply cleft than the other. If this were really the case, it is difficult to see how the wing could expand to its full extent.

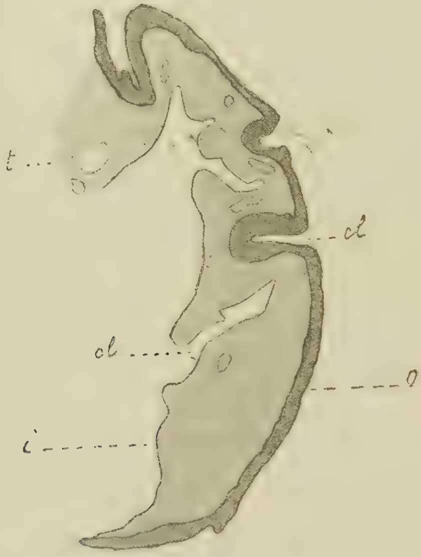

Fig. 3.—From pupa, ♀, just before the shedding of the last larval skin. × 30. The wing, in longitudinal section, is seen to be thrown into folds. The resulting deep clefts are Gonin's "découpures."
o, outer surface of wing; *i*, inner surface; *t*, trachea; *cl*, cleft.

In a larva examined eight hours after the formation of the silken girdle, the growth of the wing in the ventral direction is seen to have unfolded the loop of the envelope and brought it round to the inner aspect of the wing, where it falls into place as part of the body-wall; while its sinuosities preserve a reminiscence of the previously existing loop (Fig. 2*b*). Soon after the appearance of the deep foldings of the growing wing, there is established on the outer surface of the wing a system of numerous smaller folds, in consequence of which the outer surface presents in section a markedly sinuous outline. A chitinous cuticle invests the same surface, closely following the sinuosities. In this situation the hypoderm consists of filiform nucleated cells, attached internally to a basement membrane, and fusing by their external extremities into a finely granular layer which constitutes the matrix for the chitinous cuticle above mentioned. This system of filiform hypodermic cells, wrinkled surface and investing chitin is seen not only on the outer surface of the growing fore-wing, but also over the whole dorsal surface of the thorax in the adult larva before pupation; it foreshadows the formation of the pupal skin, and, as pointed out by Gonin, characterises those parts which in the chrysalis will be in contact with the outer air. The under surface of the fore-wing, both surfaces of the hind-wing and those parts of the body-wall which will not be external in the pupa, show fewer sinuosities; the hypodermic cells in the last-named situation are generally much shorter and more closely packed together; while the chitinous cuticle, if present, is comparatively thin. The "peritracheal spaces" figured by Gonin have now become visible. It should be borne in mind that the chitinous cuticle, thick on the outer surface, which is now seen to be investing the wings and body of the pupating larva, is not a mere case or integument for the subjacent imaginal structures; but represents, as shown by Professor Poulton,[36] a real pupal instar, which may

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[35] The growth of the wing-rudiment and gradual unrolling of the envelope are well shown in *Platyphylax* (Trichoptera) by Marshall's figures (*loc. cit.*, Pl. XXVIII, figs. 13, 13A, 15A, 16A, 16B, 18).

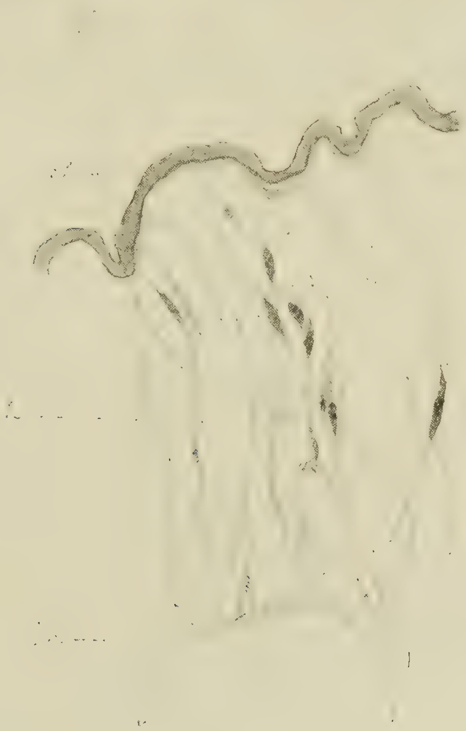

Fig. 4.—From pupa, the larval skin half shed. × 450. Section of the outer layer of the wing.
ch, chitin of outer surface; *bm*, basement membrane; *h*, hypoderm of outer surface, here consisting of nucleated fibres.

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[36] 1890, Trans. Linn. Soc. (Zool.), (2), **5**: 108.

formerly have had an independent existence. It is shed as the "pupal skin" at the time of emergence, while the true imaginal cuticle has formed beneath it.

At the time of the final shedding of the larval skin, the wings have taken a direction roughly in line with the axis of the body, and have consequently more room for growth. The deep clefts (Gonin's "découpures") are now obliterated by the expansion of the wing; the smaller folds (Gonin's "sillons"), still present, are in process of being smoothed out by the same expansion. The hypodermic cells of both surfaces preserve their filamentous character, but show signs of disintegration. The basement membrane has mostly disappeared except on the outer side of the fore-wing—the area which is covered by the chitinous cuticle. The longitudinal and lateral expansion of the wing is accompanied by a diminution of its thickness, and by the consequent approach to one another of the upper and lower surfaces; the blood derived from the general body-cavity, though perhaps not really reduced in volume, is spread out and so appears to be lessened in quantity. Many leucocytes are still present. The tracheae, whether in the body or wing, have simple walls; the remains of the tracheae of the earlier stage having now been withdrawn by the shedding of the larval skin.

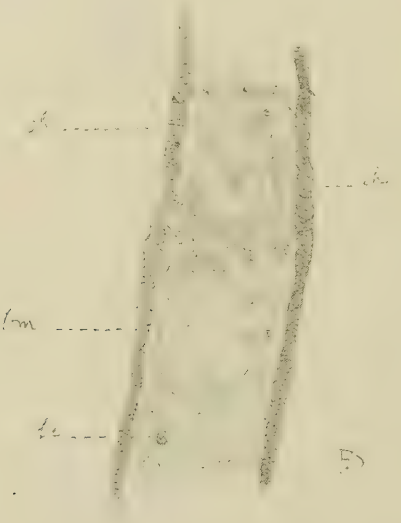

FIG. 5.—From pupa, ♀, within 1 hour after shedding larval skin. × 150. Longitudinal section of wing.
oh, hypoderm of outer surface; *ih*, hypoderm of inner surface; *bm*, basement membrane; *lc*, leucocyte.

In a pupa complete but still soft, the hypoderm cells have lost much of their filiform character. They are shorter, more numerous, and tend to be arranged in an epithelium-like row beneath the chitinous cuticle. They are largest on the outer surface of the fore-wing, partaking here of the character of the hypoderm of the dorsal body-surface. Just under the outer surface of both upper and lower wing a continuous basement membrane is present, on which the hypoderm cells rest. There is no continuous basement membrane for the inner surface; but the boundaries of the peritracheal spaces appear to represent it. The hypoderm cells of both wings and body-wall are furnished with oval nuclei. It is noticeable that the cells of the lateral pupal cornua are longer and more closely packed than those of the hypoderm in most other situations, and that the chitinous cuticle is here somewhat thickened.

At a slightly later stage, both the outer and inner surfaces of the wing have the character of a columnar epithelium resting on a basement membrane. Where a trachea runs just under the surface, the hypoderm cells are shortened, and the basement membrane consequently comes closer up to the margin. The clefts and wrinkles have now disappeared, and the contour of the wing is smoothed out.

In the pupa at a somewhat later stage, but still within twelve hours of the casting of the larval skin, the peritracheal spaces, best seen in transverse sections, are much better defined in the lower than in the upper wings. The former wings are also much thicker than the latter; containing, length for length, more blood. On the outer surface of the fore-wing the hypoderm cells form a close palisade, subjacent to the thick pupal integument. In other situations the hypoderm cells are irregularly spheroidal and in some places widely scattered. The connective tissue bounding the peritracheal spaces is seen to be continuous with the basement membrane, and to send up processes from this to the surface; to which processes, or to the basement membrane itself, the hypoderm cells adhere by prolongations directed inwards. The cells of the under surface are becoming flattened; no indication is yet visible of any differentiation of cells preparatory to scale-formation.

The thickened cuticle of the "outer" or "upper" surface of the fore-wing is in process of becoming the so-called "wing-case" of the pupa. As before mentioned, I am able to agree with Professor Poulton that the pupal integument represents an earlier stage of development than the present imago—a stage that had probably an independent existence, and that clearly approached the imaginal more nearly than the larval condition. The whole of the chitinous structures which are thrown off at the time of the exclusion of the perfect insect are probably of the like significance, no doubt with modifications. It is observable that whether seen in longitudinal or cross section, the pupal chitin, which is very thick on the whole outer or upper surface of the fore-wing, is prolonged at its edge in the same condition for a little distance on the inner or under surface. Between the fore- and hind-wing it fuses with the pupal chitin of the latter, the two together forming a single layer of thin and apparently flexible chitin, similar in character to that enveloping the inner or under surface of the hind-wing. The margin of the hind-wing, where it is in contact with the outer air, is furnished with an edging of thickened chitin like that of the whole outer surface of the fore-wing. This extends for a short distance along the margin, soon becoming merged with the thin layer of chitin enveloping the rest of the wing. The actual chitinous cuticle of the imaginal wing develops under, and independently of, the pupal chitin just described.

In a male pupa, rather more advanced but still within 24 hours of shedding the larval skin, the hypoderm cells of the upper wing, where impinged upon by a peritracheal space, besides being short tend to become hyaline, as if undergoing chitinisation. This is especially noticeable on the under surface, where a corresponding convexity, more or less marked, is often apparent, foreshadowing a future "vein." The cells of the upper surface continue to be columnar; those of the under surface are spheroidal and are now close together.

A female pupa of the same age shows similar appearances. In the peripheral part of the wing especially, no basement membrane is visible beneath the inner surface, and many bundles of connective tissue fibres run straight across from the lower hypoderm to join the basement membrane above.

In wings of the second day of pupation, there is still no indication of scale-processes. The hypodermic layer of the upper surface of the fore-wing, which is concerned with the production of the pupal cuticle, consists of cylindrical cells with large nuclei, often separated from each other by distinct intervals, ranged upon a basement membrane, and merging outwardly in a granular stratum which underlies the deeper layer of chitinous cuticle. Both this deeper and the more superficial stratum of the chitinous cuticle show a fine longitudinal striation. The pupal cuticle at what may be called the shoulder of the wing is furnished with closely-set spines projecting outwards, mostly unaffected by stains, but occasionally sharing in the staining of the cuticle. These spines are seen only on a limited area, apparently just at the junction of wing with body. I have not found them on the empty pupal case. The hind-wing at this stage is much thicker than the fore-wing. It contains a large quantity of blood, and shows fibrous strands some of which bound peritracheal spaces like those of an earlier period of development.

In the next stage, the hind-wing, though still thicker than the fore-wing, is less so than in the former condition. The basement membrane, which was at all previous stages more conspicuous and continuous beneath the hypoderm of the outer surface of the fore-wing than elsewhere, is now seen to consist of a single median membrane with fibrous ramifications passing upwards and downwards (or outwards and inwards) towards the two surfaces. This membrane, which appears to be a simple continuation, or survival, of the basement membrane of the upper (outer) surface of each wing, is more distinct in the upper than in the lower wing, which latter seems in several respects to lag behind the former in development. In both fore- and hind-wing the median or central membrane divides in certain places and reunites, thus forming spaces which appear to be identical with the already noted "peritracheal spaces" and in each of which is generally included a trachea; this arrangement being best seen when the trachea is cut transversely. When a trachea is present, the hypoderm cells bounding the peritracheal space are usually somewhat flattened and their protoplasm is usually less granular than in other situations.

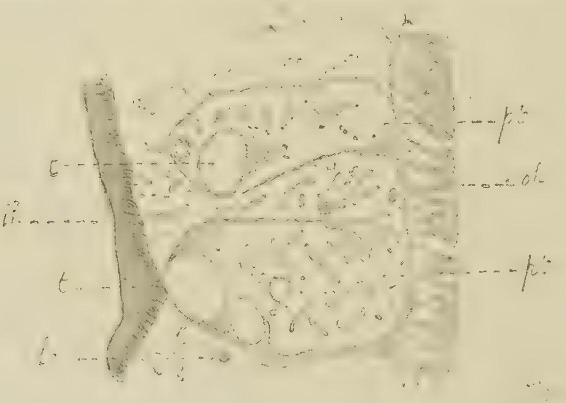

Fig. 6.—From pupa, ♂, within 24 hours after shedding larval skin. × 150. Longitudinal section of wing.
***oh*, hypoderm of outer surface; *ih*, hypoderm of inner surface; *pt*, peritracheal space; *t*, trachea; *lc*, leucocyte.**

(c) *Development of the scales.*

At regular intervals between the ordinary hypoderm cells appear the large scale-forming cells, each with a bud-like projection which is the rudiment of the future scale. This stage in a pupa of *Vanessa urticae* is well but somewhat diagrammatically figured by Schäffer (*loc. cit.*, Pl. XXX, fig. 36). The free border of both surfaces in the fore-wing has in places, when slightly out of focus, an obscurely beaded appearance; this is due to the layer of small hypoderm cells above mentioned, which are connected with processes attached to (in preparations often detached from) the central membrane. The large scale-forming cells commonly show vacuoles, as seen in Schäffer's figure. These cells in the fore-wing of a male pupa of the second or third day are seen to differ somewhat on the two surfaces. Those of the upper surface are cylindrical, forming a palisade with intervals; their nuclei are usually near the inner extremity of the cell. Those of the under surface are shorter and rather more widely separated; their nuclei are usually near the centre of the cell. The scale-processes are now spindle-shaped in outline; they arise from the scale-forming cells by long tapering footstalks, some of these may show an indication of the basal expansion which articulates with the socket in the adult wing. The scales are coarsely granular in section; when cut transversely there is no appearance of surface-ribbing. The ordinary hypoderm cells are not so easily distinguishable in this as in the preceding stage; when visible, they form a

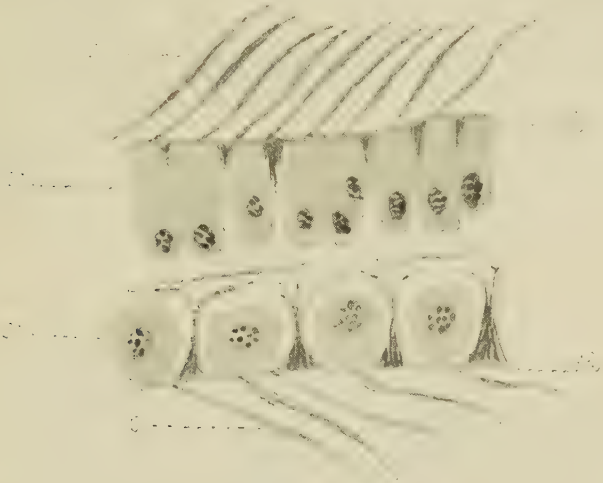

Fig. 7.—From pupa, ♂, 2–3 days after pupation. × 830.
sc, scale-cells; *s*, scale; *oh*, hypoderm of upper surface; *ih*, hypoderm of lower surface. The ordinary hypoderm appears as a beaded row of small cells.

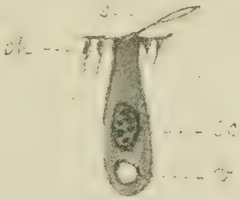

Fig. 8.—Scale-cell from upper surface; 5 days after pupation. × 830.
sc, scale-cell; *s*, scale; *oh*, ordinary hypoderm cell; *v*, vacuole.

layer running along the free surface of the wing. The fibrous elements to which they are attached pass inwardly to the central membrane; in some situations each scale-forming cell can be seen to be separated from the next by a group of ordinary hypoderm cells, generally from three to five in number. As in the preceding stage, where the central membrane divides, a space is left which usually contains a trachea. This marks the beginning of a vein. The hypoderm cells covering these spaces are somewhat altered in character; the scale-forming cells are easily distinguishable from the ordinary cells, being much larger; the ordinary cells of the upper surface are flattened and tend to become like those of the lower surface, cuboidal. Semper's rods are visible as tubes with a cellular wall and sometimes a central filament; they pass alongside the tracheae between the latter and the upper surface of the developing vein. A large marginal sac containing tracheae, free from basement membrane and fibres, lined by hypoderm but giving rise to no scales, terminates distally both fore- and hind-wing. That this appearance is not merely accidental is shown

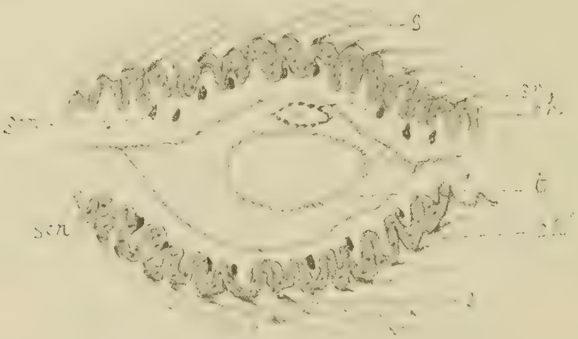

Fig. 9.—Section of vein, 4 days after pupation, ♀. × 150. The vein is cut obliquely, the chitinous walls showing transverse folds.
ch, chitin of upper surface; *ch′*, chitin of lower surface. (The dark dots in the chitin are the neuclei of ordinary hypoderm cells.) *s*, scales; *scn*, nuclei of scale-cells; *sr*, rod of Semper with central filament; *t*, trachea.

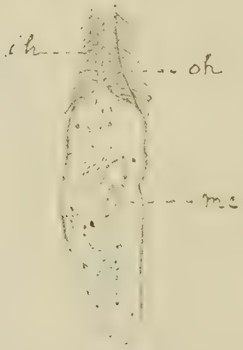

Fig. 10.—Extremity of wing, 2–3 days from pupation, ♂. × 80. Longitudinal section.
oh, hypoderm of upper surface; *ih*, hypoderm of lower surface; *mc*, marginal cavity into which the lumen of the wing expands.

by the fact that it occurs in sections cut from separate individuals, and also that the cells in the part of the wing approaching it become modified in shape. It is not the result of a slanting cut.

(d) *Stage of the formation of the final folds.*

On about the fifth or sixth day from pupation, sometimes as early as the fourth, the ordinary hypoderm cells take on a different character; they increase in size and number, and in a longitudinal section of the wing are seen to form a sharply undulating layer, the undulations being the precursors of the transverse folds which mark the wing of the freshly-emerged imago. The cells forming these undulations are rounded and finely granular, with deeply staining nuclei. The scale-forming cells still preserve their superior size; but at this stage they are displaced by the development of the hypodermic folds or undulations, and sink inwards towards the central cavity of the wing. In consequence of this accordion-like pleating, the hypodermic layer is thrown into a series of bays opening alternately outwards and inwards. For the sake of clearness, those opening outwards may be called "clefts," those opening inwards, *i.e.* towards the central cavity, may be spoken of as "arches." When these "arches" and "clefts" are fully formed, the scale-producing cells are seen to have become detached from the rest of the hypoderm; and in a section taken transversely to the hypodermic folds, each "arch" is occupied by a scale-forming cell, issuing from which can often be seen a process passing through the hypoderm to the daughter scale, the base of the latter being now enclosed in a socket. The scale-forming cell, though liable to be displaced in the course of preparation, is usually to be found lying close to the proximal limb of the arch. Its process follows the curve of the arch until it meets the socket of its own scale, which occupies the summit of the arch. The socket, like the scale in its final form, appears to be a chitinous excretion of the mother-cell.

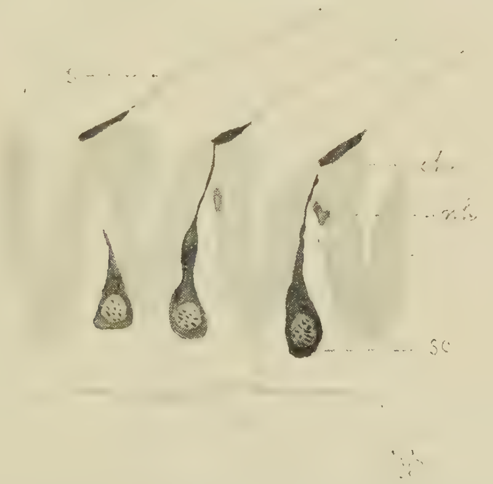

Fig. 11.—Longitudinal section of upper surface of wing, 4 days after pupation, ♀. × 830.

ch, chitin of upper surface; *nh*, nucleus of ordinary hypoderm cell; *sc*, scale-cell; *s*, scale. The middle one of the three scale-cells is seen to be in actual connection with the socket of the corresponding scale.

The arrangement just described of cells and scales is visible without difficulty in the female wing and on the under surface of the wing of the male. On the upper surface of both fore- and hind-wing in a male specimen it is somewhat complicated by the presence of the developing scent-scales with their underlying mother-cells. In the latter situation, as in the former, each arch has an ordinary scale with socket; but at the bottom of each cleft is to be seen the mother-cell, socket, accessory disc and more or less of the footstalk and lamina of a scent-scale. There is thus, in a longitudinal section of the upper surface of the male wing, a regular alternation of the two kinds of scale, the one kind occupying the summits of the arches or ridges, the other the cavities of the clefts or depressions between the ridges. It follows from this that for equal areas the scales are more numerous on the upper surface than on the lower. But as in a transverse section of the wing, the ordinary scales are seen to be more closely packed in their lateral rows than the scent-scales, the proportion is somewhat less than 2 : 1. The ordinary sockets are narrow and conical or cylindrical; the scent-scale sockets are large and wide with everted lips. The accessory discs of the scent-scales are linear or oval in section according to the plane in which they are cut; in the latter case their contents appear to be granular.

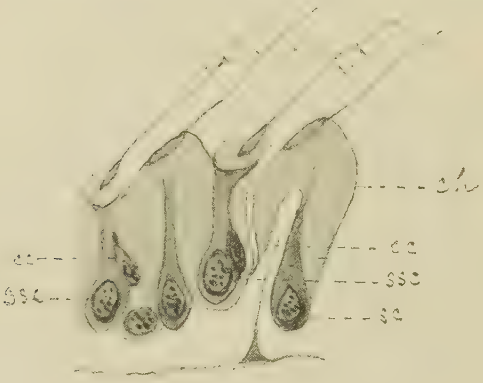

Fig. 12.—Longitudinal section of upper surface of wing, 8–9 days after pupation, ♂. × 830.

ch, chitin of upper surface; *sc*, ordinary scale-cell; *ssc*, scent-scale cell; *cc*, companion cell of scent-scale cell. The scent-scales with their sockets are seen to occupy the furrows between the ridges which bear the ordinary scales.

When the undulations are fully established, the marginal sac above mentioned is taken up into the general fabric of the wing; its lumen, previously expanded, becomes narrowed to that existing between the two layers in the rest of the wing. It is now well provided with scale-cells, some of which are unusually large and give rise to the elongated scales or " hairs " which form the marginal fringe. The scent-scales persist nearly up to the margin.

On the convex aspect of each cleft, looking towards the cavity of the wing, is usually to be seen a quantity of fibrous material derived from the hypoderm; this is prolonged by one or more strands to reach the central membrane, where it often meets a similar prolongation from the corresponding cleft of the other surface. These fibrous elements are very apt to be broken and displaced in the course of preparation.

(e) *The later pupal stages.*

By the sixth day from pupation some other features appear for the first time, or become more easily visible. Where the plane of the section passes along the course of a vein, the hypodermic arches and clefts become more clearly defined. Their constituent cells, much more evident than in other parts of the wing, have a somewhat hyaline appearance, and their nuclei are sharply outlined. The clefts are laterally compressed, their two sides almost touching, and the arches are widened in compensation. The clefts bear no scent-scales, for which indeed there would be no room. A thin layer of highly-refracting chitin follows the hypodermic folds on their outer aspect, covering the tops of the arches, and lining both sides of the narrowed clefts. Within the cavity of the vein are to be found, side by side, a trachea and a rod of Semper, the latter always running between the trachea and the upper surface of the wing. Vein, trachea and rod are obviously independent structures, entirely distinct from one another. The rods, which continue to retain their character of tubes with a wall composed of a single layer of cells, are dilated at the base of the wing into large cavities. In transverse section their walls sometimes show slight irregularities projecting into the lumen; these may perhaps represent the "Bäumchen" figured by Schäffer in the wing of *Vanessa urticae* (*loc. cit.*, Pl. XXX, fig. 37). The basal dilatations of Semper's rods have granular material in their lumen; their cellular coat is in places distinctly connected with the basement membrane of the upper surface. They usually contain, as in Schäffer's figure, a filamentous central cord; which sometimes appears to be flattened and membranous and sometimes separates out into distinct strands. Where a trachea branches, the accompanying rod of Semper branches with it. In many sections another rod or cord, narrow and looking tubular in places, runs parallel with Semper's rod just under the basement membrane. Like the trachea and Semper's rod, it takes a straight course, not following, as do the walls of the veins, the transverse folding of the wing. In the basal portion of the wing, the main tracheal branch emits fine tracheal capillaries. Where the surface of a scale is

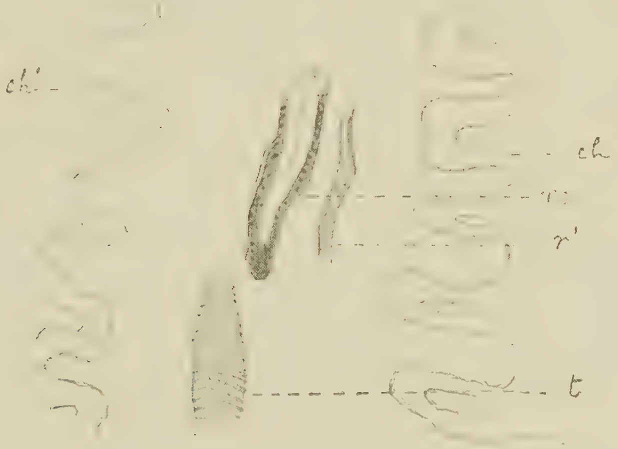

Fig. 13.—Longitudinal section of vein in ♂ pupa of 6 days. × 450. *ch*, chitin of upper surface; *ch'*, chitin of lower surface; *rs*, rod of Semper cut obliquely; *t*, trachea; *r'*, additional rod.

visible in the preparation, it is seen to be regularly ribbed; the scale itself being devoid of the granular contents present at the earlier stages.

In addition to the nucleus which belongs to each scent-scale, there is sometimes to be seen a smaller nucleus, also spheroidal, on the distal aspect of the former, and usually nearer the surface. It is less like the nuclei belonging to the mother-cells of the ordinary scales than are the formative nuclei of the scent-scales. The small cell to which it belongs has perhaps a different function; possibly to provide the scent-bearing secretion (Fig. 12 *cc*). At about the eighth or ninth day these smaller cells, which are quite distinct from the general hypoderm, are in places very easily visible; they appear often to send processes into the socket of the scent-scale to which they belong. At this, as in the previous stage, the nucleus of the main scent-cell as well as of its companion small cell often lies somewhat nearer the surface of the wing than does the row of ordinary scale-cell nuclei; and the "small" or "companion" cell does not always seem to be quite clear of the plicated hypoderm layer. As one would expect, no indication of similar "companion cells" is to be seen in connection with the under surface of the wing, which surface has no scent-scales. On both surfaces tapering processes are often still visible, passing from the nuclei of the ordinary scale-forming cells to the sockets of their daughter scales.

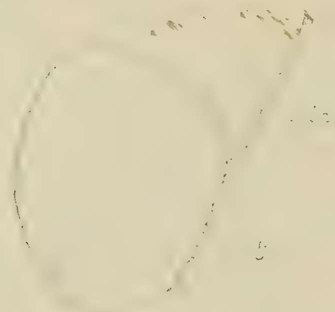

FIG. 15.—From vein, 8–9 days after pupation. × 450.
t, trachea; *tc*, tracheal capillary branch.

(f) *The last stage before emergence.*

In a wing just before emergence, the cells seem to have lost all connection with their daughter scales, being mostly reduced to mere nuclei. The hypoderm shows a thick layer of chitin in the section of a vein, whether longitudinal or transverse, thickest on the under surface. The chitin is here underlain by a definite layer of hypodermic cells. In other parts of the wing, away from the veins, the hypoderm folds are partly chitinised, obscurely granular in appearance, but showing few or no signs of cellular constitution. The exposed limb of the scale-socket is more deeply stained and perhaps thicker than the engaged limb. Tracheae, apparently degenerate, run in the veins. Semper's rods are still visible, running as before between the remains of the tracheae and the upper surface of the wing. They are somewhat attenuated, and now appear to have a definite connection with the basement membrane of the upper surface. Like the tracheae, they do not share in the folding of the hypoderm. The veins as seen in transverse section are bounded laterally by fibres taking a curved course between the two surfaces of the wing so as to include the cavity of the vein. These fibres are hypodermic and nucleated. Nuclei are seen at both the upper and under extremities of the fibres, but there is only one nucleus to each fibre. In the fibres forming the boundary of the vein, the nucleus appears to be always at the upper extremity. Schäffer's figure of a transversely cut vein in *Vanessa* (reproduced by Dr. Sharp, *loc. cit.*, p. 330) seems to show some fibres with two nuclei; this appearance is probably deceptive. The stout chitinous arch of the lower or underside wall of the vein is occupied by a bunch of well-developed elongated hypoderm cells, resting on a basement membrane, and spreading out in the form of a rosette. (The definite ring seen in Schäffer's figure is formed of basement membrane and hypodermic fibres.) The two layers of the wing, upper and under, are close together; there appears to be a basement membrane for each which does not follow the folds, but bridges the base of the "arches." Crossing the cavity between the upper and under layers are many bundles of fibres; these appear to be derived from and continuous with the basement membranes. The bundles divide the lumen of the wing-cavity into circular or oval spaces, visible as such in both longitudinal and transverse sections.

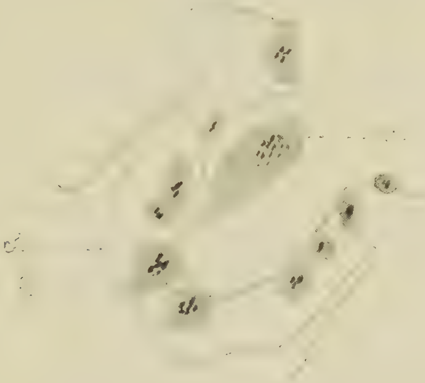

Fig. 14.—Section of lower surface wall of vein, 8–9 days after pupation. × 1380. *ch′*, chitinous lower wall of vein; *h*, ordinary hypoderm cell; *sc*, scale-cell.

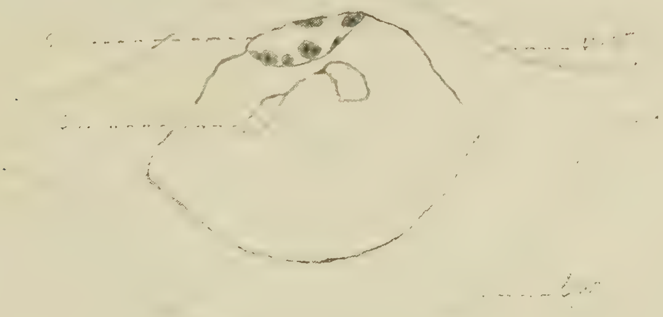

Fig. 16.—Vein; transverse. × 450. 8–9 days after pupation. *uw*, upper wall of vein; *lw*, lower wall; *rs*, rod of Semper; *t*, trachea (degenerate).

(g) *Expansion of wings after emergence.*

Immediately after emergence from the pupa, in all ordinary cases the wings begin to expand. This expansion takes place by the unfolding of the "clefts" and "arches" seen in a longitudinal section of the wing before emergence, and also of the narrower and shallower clefts which, at right angles with the former, separate the scale-sockets and scales of each transverse row. The former operation provides for the growth of the wing in length, the latter for that in breadth. From the longitudinal expansion results the arrangement of ordinary and scent-scales in alternate rows, as seen in the wing of the adult male. As

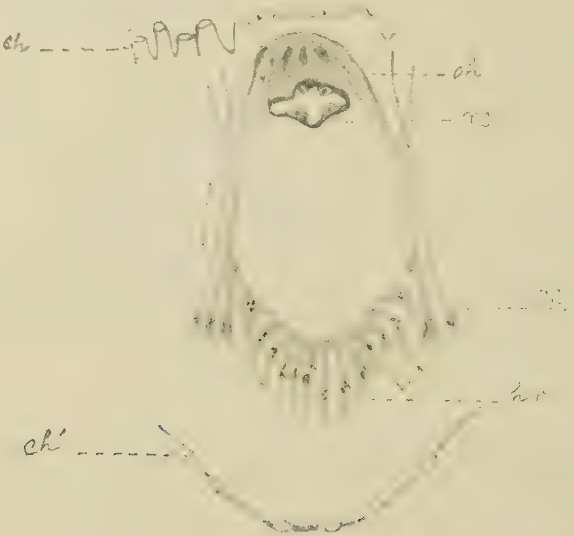

FIG. 17.—Vein transverse, ♀. × 450. About to emerge.
ch, chitin with scale-sockets, upper surface; *ch'*, do., lower surface; *oh*, hypoderm, upper surface; *ih*, do., lower surface; *hr*, hypodermic "rosette"; *rs*, rod of Semper. Note absence of trachea.

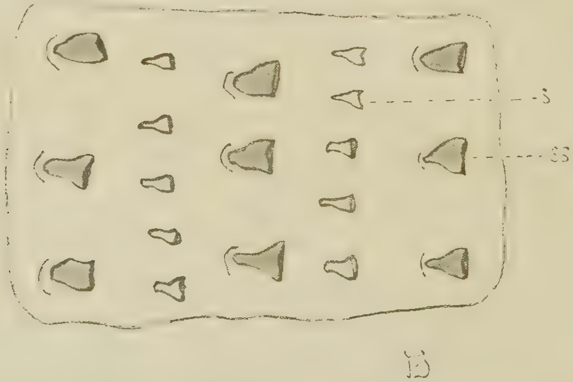

FIG. 19.—Portion of wing of adult ♂, with sockets. × 450.
s, socket of ordinary scale; *ss*, socket of scent-scale. The sockets are seen to be arranged in alternate rows.

neither trachea nor Semper's rod takes part in the folding of the including vein, it appears to follow that neither of these structures can have place in the peripheral part of the vein when the latter is straightened out. It has already been shown that the trachea has begun to degenerate before the time of exclusion; and when the wing has begun to expand, neither trachea nor rod as such is to be seen in the cross section of a vein, except occasionally near the base.

As a result of the straightening of the folds in the parts of the wing included between the veins, the bundles of fibres which pass from surface to surface across the cavity between them are resolved into their constituent fibres. These accordingly are now distributed at approximately equal distances throughout the cavity. The expansion of the wing, which is probably set going by fluid pressure from the interior of the thorax (Semper, Günther), is no doubt prevented by the presence of these fibres from unduly separating the upper and under surfaces in the areas between the veins (Illig). There being at this stage no actual partition between the interior of the vein and the cavity of the wing, the fluid pressure cannot be confined to the former, but must tend to the inflation of the wing generally. Whether, as is sometimes stated, the final flattening of the wing and the coherence of its two surfaces by the obliteration of the cavity between them is due to the contraction of the separating fibres, appears to me doubtful. In sections of the partly expanded wing taken soon after emergence, I find no appearance in the fibres distinctly suggesting contraction. They have, as already stated, lost their collection into bundles, and now run individually from side to side of the cavity. In many places they are ruptured. The first effect of fluid pressure would be to separate the surfaces, but the amount of blood present within the thorax at the time of exclusion would not be sufficient to bring about a very great separation, even in the absence of the fibres; and it appears to me worth considering whether the actual unfolding of the wing, and especially the divergence of the principal veins as they lengthen, may not help in bringing the two surfaces together. Perhaps also whatever there may be of elasticity in the chitinous folds can be taken into account as a possible factor in the expansion of the wing and in its final condition.

In a wing about one-quarter expanded, each vein in transverse section is seen to be lined by a complete ring of nucleated hypoderm fibres; this ring passes between the lumen and " rosette " beneath, and above either fuses with the remains of Semper's rods, where these persist, or is continued between the latter and the hypoderm of the shallow chitinous arch of the upper surface. The nuclei of the fibres forming the ring appear to be in series with those of the rosette; and the fibres themselves are like those derived from the basement membrane, which is all that remains of the hypoderm in other parts of the wing. Transverse sections show the lateral clefts between the scale-sockets gradually opening out and becoming obliterated. The scale-forming cells have generally disappeared, but some nuclei appear to be present in the sockets of the scent-scales.

In a wing about three-quarters expanded, the fibres connecting the two surfaces are generally wavy, but do not look contracted and are often broken. They frequently appear to be membranous rather than fibrous. The transverse wrinkles or clefts between the scale-sockets are almost smoothed out. In the veins the rosettes are reduced in bulk, and, as might be expected, traces of Semper's rods are only occasionally to be seen. A group of hypoderm cells, corresponding with the rosette of the under surface, but naturally smaller, underlies the shallow chitinous arch of the vein above.

(h) *The wing in the adult.*

In the fully adult wing that has been used for flight, the two surfaces are almost everywhere in complete union, there being, except for the veins and their immediate neighbourhood, little or no trace of the cavity between them. The veins in transverse section show a chitinous ring, thicker and strongly convex on the under or inferior surface; on the upper or superior surface flat and less completely chitinised. Each extremity of the chitinous arch forming the inferior wall of the vein expands as it reaches the general level of the wing into a basal triangular portion, which sometimes fuses with the flattened superior wall, and sometimes, especially near the base of the wing, leaves a narrow interval which extends for some little distance laterally between the two surfaces. Within the outer chitinous envelope there is another ring, the walls of which, imperfectly if at all chitinised, have a granular appearance and in some situations seem to be cellular. This inner ring is the transverse section of a tube, foreshadowed at an earlier stage by the hypoderm and fibrous processes lining the vein, the wall of which tube is at some levels free, at others fused with the chitinous tube within which it lies. A thin protoplasmic film extends from this inner ring into the narrow interval above mentioned. The part of the inner ring from which the lateral film arises is seen in transverse section as a triangular expansion of the wall of the ring on each side, but marked off from the central part by a thin wall. In the more distal parts of the wing, each of these lateral expansions is furnished with a central cavity, so that in transverse section the inner ring is threefold, consisting of a central and two lateral divisions. The central division varies in size and shape at different levels, being frequently encroached upon by the enlarging lateral divisions, and presenting in many cases a circular or goblet-shaped outline, connected by a narrow footstalk with the wall of the upper surface. In longitudinal sections of the adult wing, the sockets of the ordinary scales, and, on the upper surface in a male specimen, of the scent-scales, are seen to be projecting at an acute angle from the general level of the wing. The sockets of both kinds of scale contain granular material staining deeply with haematoxylin, in which an apparent nucleus is occasionally present.

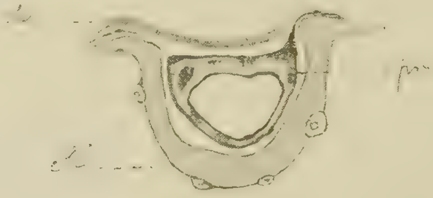

Fig. 18.—Vein transverse. × 450. Adult.
ch, upper chitinous wall; *ch'*, lower do., with scale-sockets; *pr*, protoplasmic ring.
Note absence of trachea.

(i) *Tracheae in the adult wing.*

It is observable that though, as far as my observations extend, the veins in the adult wing of *P. rapae* contain no tracheae, this is not universally the case throughout the Lepidoptera. Fritz Müller in 1878 described and figured air-vessels proceeding from certain veins in the hind-wing of the male *Antirrhaea* *archaea*, Hübn., and distributed to the scent-patches.[37] Spuler observed a trachea in a vein of *Triphaena pronuba*.[38] The present writer has described tracheal branches in connection with the scent-patches in *Teracolus fausta*, Oliv., *Catopsilia florella*, Fabr., *C. pyranthe*, Linn., *Colias croceus*, Fourcr. (*edusa*, Fabr.).[39]

In the hind-wing of an adult specimen of *Colias edusa* that has been denuded of scales, tracheal branches, themselves branching, can be seen to traverse the area occupied by the scent-patch in the angle between the costal and subcostal veins. Sections show that in both of these veins the main tracheal branch is still present, but in a collapsed and degenerate condition. In fortunate sections the fine tracheal branches above mentioned can be seen to be emitted from the degenerated trachea of the subcostal vein, and to run between the chitinous membrane of the lower surface of the wing and the glandular layer of living secreting cells belonging to the scent-patch.

The cellular tube above spoken of as lining the chitinous walls of the veins in *P. rapae*, and consequently appearing in cross section as a ring, is also to be seen in *C. edusa*, where in the region of the scent-patch the protoplasm of the ring is similarly continued both ways laterally between the surface membranes of the wing. This protoplasmic extension is largest in amount on the anterior aspect of the subcostal vein, where the surface membranes are separated to give room for the scent-cells. Where this lateral prolongation intervenes, the chitinous sheathing of the vein is, of course, incomplete.

In sections of the fore-wing of *Gonepteryx rhamni*, Linn., and *G. cleopatra*, Linn., taken near the end of the cell, there is visible a similar prolongation of protoplasmic material from a tripartite ring in the vein laterally into the wing generally, between the chitinous surfaces. Accumulations of protoplasm underlie the sockets of the specialised scales of the upper surface; and also, though less in quantity, below the sockets of scales of the lower surface. In some sections the protoplasmic film can be traced from the ring in the vein up to the sockets of the scales.

In the scent-patch of *Colias edusa* the scent-scales can be distinguished from the ordinary scales by the possession of a " collar " or trumpet-shaped expansion of the lamina just where it joins the footstalk. Each socket of an ordinary scale is underlain by a nucleated cell, smaller than the scent-cells and differing from them in character.

SUMMARY.

1. The wing of a Lepidopterous insect originates in an invagination of the larval hypoderm (Dewitz, Pancritius, Schäffer; *contra* Semper).

2. The wing-rudiment results from a secondary infolding of the upper layer of the original invagination. The envelope is formed by a folding of the lower layer of the original invagination round the wing-rudiment (Ganin, Dewitz).

3. Tracheae and blood enter the wing-rudiment from the body-cavity through the secondary infolding of the upper layer of invagination (Ganin, Dewitz, Pancritius; *contra* Landois, who supposes the tracheae of the wing to be derived from cells of the actual wing-rudiment, which he regards as an essentially tracheal structure).

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[37] 1878, Arch. Mus. Nac. Rio de Janeiro, **3** : 1–7. English translation by Mr. E. A. Elliott in 1912, *Butterfly-hunting in Many Lands*, by Dr. G. B. Longstaff, p. 634, Pl. E, figs. 8, 9.

[38] 1892, *Z. wiss. Zool.*, **53** : 623.

[39] 1911, Rep. Brit. Ass., **1911** : 419. 1912, *Trans. 2nd Ent. Cong.*, pp. 340–41.

4. The wing becomes external by extrusion of the wing-rudiment through the original aperture of invagination (Dewitz, Pancritius, Gonin, Mercer).

5. The envelope is not destroyed (Dewitz; *contra* Ganin, Gonin), but is unrolled and straightened out by the prepupal growth of the wing; thus coming into line with the general hypoderm, and taking its own place as a portion of the ventral body-wall (similarly in PHRYGANIDAE, *teste* Marshall).

6. It follows that the space between the wing-rudiment and its envelope is a relic of the original cavity of invagination; that both surfaces, upper and under, of the adult wing represent a part of the original floor of that cavity; and that the interior of the wing, and the space included within the outermost loop of the envelope, are diverticula of the general body-cavity.

7. In the process of larval growth, the rudimentary wing is thrown into a series of deep folds (Gonin's "découpures"); somewhat later on, a system of smaller wrinkles (Gonin's "sillons") appears on the outer surface of the fore-wing. These latter wrinkles become invested with the chitin of the pupal skin; both systems of clefts or wrinkles are obliterated by the expansion of the wing at the shedding of the larval skin.

8. The veins of the adult wing are foreshadowed by sheaths of basement membrane ("peritracheal spaces"). The hypoderm cells investing these sheaths undergo modification.

9. The actual chitinous cuticle of the imaginal wing develops under and independently of the pupal wing; the latter, as shown by Poulton, represents a real pupal instar, which may formerly have had an independent existence.

10. The large scale-forming cells become distinguishable on the second or third day of pupation. They are hypodermic in origin (Schäffer, Mayer), and are separated from each other by ordinary cells of the hypoderm.

11. Semper's rods become visible at about the third day as tubes with a cellular wall. They are quite distinct from the tracheae (Semper, Landois, Schäffer; *contra* Mercer, Woodworth), lying between the tracheae and the upper surface of the wing.

12. At the fourth or fifth day from pupation the ordinary hypoderm cells proliferate and take on a different character. A regular series of transverse undulations appears, and the scale-forming cells, becoming detached from the rest of the hypoderm, sink inwards towards the central cavity of the wing.

13. On the upper surface of both fore- and hind-wing in a male specimen of *Pieris rapae* can now be seen the developing scent-scales with their sockets and underlying mother-cells. These occupy the furrows, loops or "clefts" of the undulations as seen from the upper surface, while the ordinary scales start from sockets set along the ridges or "arches" between the furrows. There are ordinary scales, but no scent-scales, on the veins.

14. The walls of the veins, strongly chitinised, follow the transverse folding of the wing; the tracheae and Semper's rods take a straight course, and are consequently left behind when the wing unfolds. In the species examined (*P. rapae*), neither trachea nor rod is seen in the adult wing. In other species of PIERIDAE, relics of the tracheal system persist in connection with the patches of scent-scales.

15. Just before emergence, the two surfaces of the wing are seen to be bound together by numerous bundles of fibres derived from the upper and under basement membranes, which do not follow the undulations of the hypoderm. These bundles, on the expansion of the wing after exclusion, become resolved into their constituent fibres, which pass across the cavity of the wing at

approximately equal distances. Whether they undergo contraction seems doubtful.

16. The flattening of the wing after emergence takes place in the longitudinal direction by the unfolding of the undulations seen from the fourth or fifth day of pupation onwards; in the transverse direction by the smoothing out of shallower clefts, at right angles to the former, between the sockets and scales of each transverse row. From the longitudinal expansion results the arrangement of ordinary and scent-scales in alternate rows as seen on the wing of the male adult.

17. In the fully adult wing the two surfaces are in complete union; the intervening cavity with its contents, except for the veins, and a small area adjacent to the veins, having become entirely obliterated.

TWO SPECIALLY SIGNIFICANT EXAMPLES OF INSECT MIMICRY

By Edward B. Poulton, D.Sc., F.R.S., Fellow of Jesus College, Oxford, and Hope Professor of Zoology in the University.

[Read 6th May, 1931.]

Plates XIV, XV.

Mimetic resemblance independent of affinity is of course well known, especially among the Lepidoptera with striking colours and patterns; indeed, "There is no end to it," as the late Osbert Salvin once said to the writer. Many students of evolution, both naturalists and followers of other sciences, believe that these resemblances and the circumstances in which they are manifested can only be understood in the light of the Darwin–Wallace hypothesis of Natural Selection. Others, unconvinced by this interpretation and having, so far as I am aware, no other to offer, await some unknown solution which appears to be brought no nearer by an ever-accumulating mass of fresh observations. It therefore occurred to me that an illustrated account of two remarkable examples which point with quite exceptional clearness to an evolutionary history based on selection might perhaps induce some of our agnostic friends to assume a more positive and hopeful attitude. The two coloured plates, essential in support of the evidence, and in order to carry conviction, have been made possible by a grant from the Fund for Promoting the Study of Organic and Social Evolution, presented to Oxford University by my old friend Professor James Mark Baldwin. I wish also to thank Miss O. F. Tassart for the care and skill with which she prepared the excellent drawings and the engravers for the successful reproductions.

A feature in the mimetic resemblance of Papilio laglaizei, *Depuiset, to the Uraniid moth* Alcidis agathyrsus, *Kirsch.*—I owe the opportunity of bringing forward this striking instance, to the kindness of Dr. Karl Jordan who has so often given me much help in my work. The Uraniid moth *Alcidis agathyrsus* and its mimic *Papilio laglaizei* inhabit New Guinea and Waigeu, while in Aru the butterfly, originally named from one of these islands as *alcidinus* by Butler, is said by him to be "an exact copy on the upper surface of *Alcidis aruus* of Felder." * Dr. Jordan informs me that the British Museum specimen of *alcidinus* from Aru does not differ from the New Guinea *laglaizei*, although the *Alcidis* is slightly different from *agathyrsus*.

Dr. Jordan, in Seitz, 1927, **9**: Indo-Australian Rhopalocera, 46, 47, places the *laglaizei* Group of Swallowtails before the Groups of *anactus* and *demoleus* and immediately after that of *castor*, all belonging to Section B, the Fluted Papilios, to which *P. machaon* belongs. According to A. S. Meek, on whom Dr. Jordan has relied for information, *laglaizei* is not rare at the S.E. extremity of British New Guinea, but uncommon elsewhere throughout the island. The *Alcidis* model and butterfly mimic "fly together round the tops of trees, but the Uranid is much commoner than the Papilio." Both, taken on the same day, 9 August, 1912, at Waigani, Milne Bay, S.E. New Guinea, were kindly presented to the Oxford University Collection by Mr. G. M. Carson—

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* 1883, *Ann. Mag. Nat. Hist.*, (5) **11**: 423.

part of a long series of valuable specimens from the same area. Other examples of model and mimic taken by Native collectors, probably on the E. side of Geelvink Bay, Dutch New Guinea, were kindly presented by Lord Rothschild.

Coming now to the mimetic resemblance between the butterfly and moth, the simple upper surface pattern, similar in both insects, is made up of beautiful, pale greenish blue, iridescent markings on a black ground, the short, broad-based "tail" of the hind-wing being whitish blue. Thus, as Dr. Jordan states, "the resemblance to *Alcidis agathyrsus* is surprisingly faithful on the upper surface," while, as may be seen by comparing figs. 1 and 2 on Plate XIV, "the under surface differs considerably from that of the model, but bears a usually very conspicuous orange spot which corresponds to the orange-coloured underside of the abdomen of *Alcidis*." This is the essential feature, so well illustrated on Plate XIV, and pointing so clearly to an evolution due to selection by enemies whose actions were determined by the sense of sight. Looking at the model as shown in fig. 1 we may feel confident that, in the resting position, the moth hangs, probably from a twig, with drooping wings so that the orange under surface of the abdomen is higher than any part of the wing-pattern and, strongly contrasted with all others, forms by far the most conspicuous and easily remembered marking on the insect—a typical aposeme. Now if we suppose, as some have done, that mimetic resemblance is brought about by model and mimic reaching independently the same stage of development in the feature which exhibits the likeness, then, quite apart from the difficulty imposed by the immense difference between the two insects, it is obvious that such an interpretation implies that the orange patch should have appeared on the abdomen of the butterfly and not in two halves on the hind-wings. But if it had so appeared it would have been invisible when the abdomen is enclosed between the two hind-wing grooves, as it is in the Papilios. These grooves are clearly shown in fig. 2, representing the hind-wings strained apart—a position unnatural in life. In fig. 3 they are shown with the grooves closed over the body and the two halves of the orange patch united. This is probably the appearance in the natural resting position, hanging with drooping wings like the model. It is much to be hoped that some naturalist who has the opportunity will test these conclusions by observing the positions during prolonged rest of both model and mimic. It appears to be probable that if the wings of the resting *Papilio* hung vertically, a chink would open between the hind-wings, and the orange patch would divide. I think it is likely, however, that the mimetic resemblance has been increased by the butterfly assuming when at rest the more moth-like position of drooping and not vertically hanging wings.

It is interesting to find that the only other species in the *laglaizei* Group—*Papilio toboroi*, Ribbe, from Bougainville, Solomon Islands, and rather common in low situations in the interior, resembles, in the absence of an *Alcidis*, a Geometrid moth, *Dysphania pilosa*, Butler, which is apparently common in the island, and "in spite of its smaller size, bears quite the same aspect as the *Papilio*" (*Ibid.*, p. 47). The species of *Dysphania* are conspicuous day-flying moths well known to be mimicked in other localities.

It should be added that similar although less striking methods of resemblance to models are found in other species. Thus, among the especially distasteful and conspicuous Papilios of the *Aristolochia* (or *Pharmacophagus*) Section A, certain species with red markings on the body are mimicked by Papilios of another Section (the Kite Swallowtails, or *Cosmodesmus*) and by certain

Pierines (*Euterpe*), with red on the part of the hind-wings which covers the dark body and thus simulates a red body-marking, also often with red on the extreme base of one or both wings which is close to the body.

False cocoons of parasites spun or otherwise formed by caterpillars outside their own cocoons.—Our knowledge of these most remarkable adaptations is almost entirely due to the acute observations conducted by Dr. W. A. Lamborn, O.B.E., when residing at Oni, about 70 miles E. of Lagos. The most interesting of them, represented, natural size, on Plate XV, was described in *Proc. Ent. Soc. Lond.*, **1911** : xcv, ci, and 1930, **5** : 13. In fig. 1, eight reddish cocoons of a Bombycid moth, *Norasuma kolga*, Druce, are represented on the under surface of a leaf. Before constructing its cocoon the caterpillar spins a loose web bearing several oval masses of yellow silk which closely resemble the cocoons spun by parasitic larvae of BRACONIDAE, after devouring their host and making their way to the surface. Within this network the Bombycid caterpillar then spins its own dense cocoon and reddens it, probably by means of a nitrogenous fluid excreted by the Malpighian tubules and discharged from the anus –another example of the advantageous use of a waste product; for the little yellow masses stand out far more conspicuously because of their reddish background. A female and three males which emerged from four of the cocoons are represented in figs. 2, 3, 5, and 6, respectively, also a female Ichneumonid parasite in fig. 4. This insect, determined by Mr. D. S. Wilkinson[*] as *Mesostenus basimacula*, Cam., had developed from a solitary larva which, after devouring its host, pupated within one of the reddish cocoons and not on the surface after the manner of the BRACONIDAE. It has been suggested that these false cocoons are adapted to deceive the female parasite and thus prevent her from ovipositing in the Bombycid caterpillar or pupa. This interpretation is most improbable because such females are guided by other senses as well as by sight, if indeed sight is employed at all for this purpose. Furthermore, the parasitic larvae which emerged and spun yellow cocoons like the pretence ones represented on Plate XV, would have been hatched from eggs deposited at a much earlier period and probably far back in the life of the Bombycid caterpillar.

The tough wall of a Braconid cocoon, together with the small size of the enclosed larva or pupa, probably explains the meaning of the bright yellow colour as a warning to insectivorous Vertebrates that it will be difficult to reach the food within and that when reached it will be very scanty. A few experiments, perhaps a single one, would teach two lessons—(1) that a cocoon bearing these parasites in their silken cases only encloses a shrunken skin or empty shell and is not worth opening, (2) that the parasitic cocoons are also unworthy of attention. The aposematic conspicuousness of the latter is advantageous to the Bracons because enemies are all the more readily discouraged from making attempts which would incidentally lead to the destruction of some of them. Hence the obvious advantages conferred by false cocoons of parasites when mistaken for real ones.

The above line of reasoning is supported by observations which prove that birds are quick to appreciate the difference between objects which may or may not provide food or may provide different qualities of food. This is well shown by the fact that they will open " bullet galls " which contain the insect, but save themselves the trouble of opening empty ones, guided by the small hole of exit or by some difference in their vibration when tapped with the beak (*Ibid.*, 1928, **3** : 50–52; 1929, **4** : 10). Such observations teach us that birds have to work for their living and cannot afford to waste time and effort upon worthless objects. The behaviour of birds, as well as mammals and reptiles, towards distasteful insects with warning colours also proves that their reactions are such as are likely to benefit the relatively few species which construct false parasitic cocoons.

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[*] *Bull. Ent. Res.*, **21** : 284.

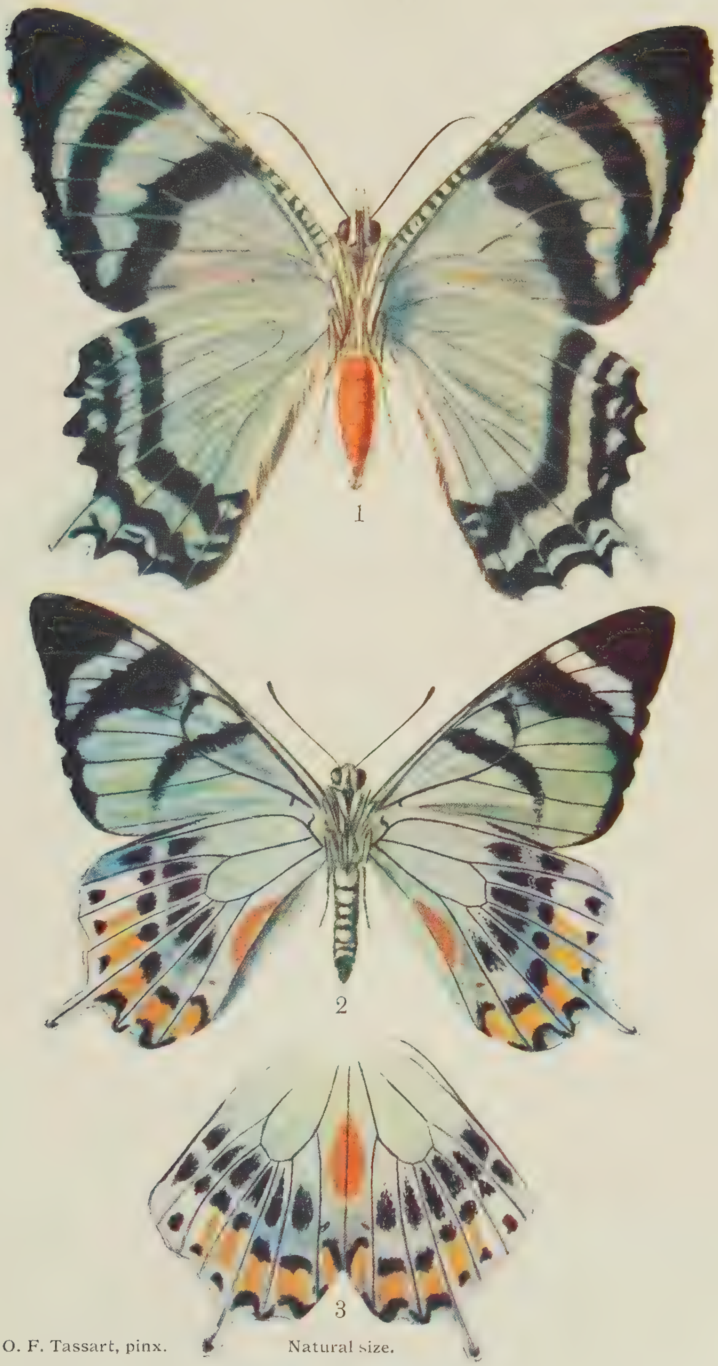
The interpretation here offered is also strongly supported by the fact that false cocoons are made in an entirely different manner by the larvae of certain other moths. The cocoon of the W. African *Deilemera antinorii*, Oberth. (CALLIMORPHIDAE), was observed by Dr. Lamborn to be covered by numbers of little creamy-white or yellowish spheres which so forcibly suggested a mass of Braconid cocoons, that he was at first deceived. Later on he observed that the apparent cocoons were really little spheres of bubbles ejected one at a time *per anum*, by the larva while it was spinning its cocoon, but ceasing work during the actual passing of a sphere. When two or three have accumulated "the larva turns round, weaves a few turns of silk round one and drags it away to the required position. . . . It then fixes it by a few further turns of silk, and then removes the remaining spheres one by one in a similar way. . . . I think the silk serves as a handle" (1911, *Proc. Ent. Soc. Lond.*, **1911** : xcvi, xcvii; see also xlvi, lv; **1913** : v).

The late Mr. G. F. Leigh, of Durban, also observed the same procedure in the E. African *D. leuconoe*, Hopff., and was at first similarly deceived, for, in his own words, "When I first bred this species I actually threw away three or four cocoons of the first lot, thinking that Ichneumonid [Braconid] parasites had emerged from the larvae." He also observed that the larva, like that of the Bombycid *N. kolga*, was attacked by a true Ichneumonid parasite; also that another *Deilemera*, which he observed in the Comoro Islands, similarly ejects false Bracon cocoons (*Ibid.*, **1911** : xcvii, xcviii).

Similar but much smaller bodies, almost certainly passed by the anus, are found on the cocoons of the Tineid genus *Marmara*, as described, with references to the original records, by the late Mr. J. H. Durrant (*Ibid.*, xcviii, xcix; **1912**: cix).

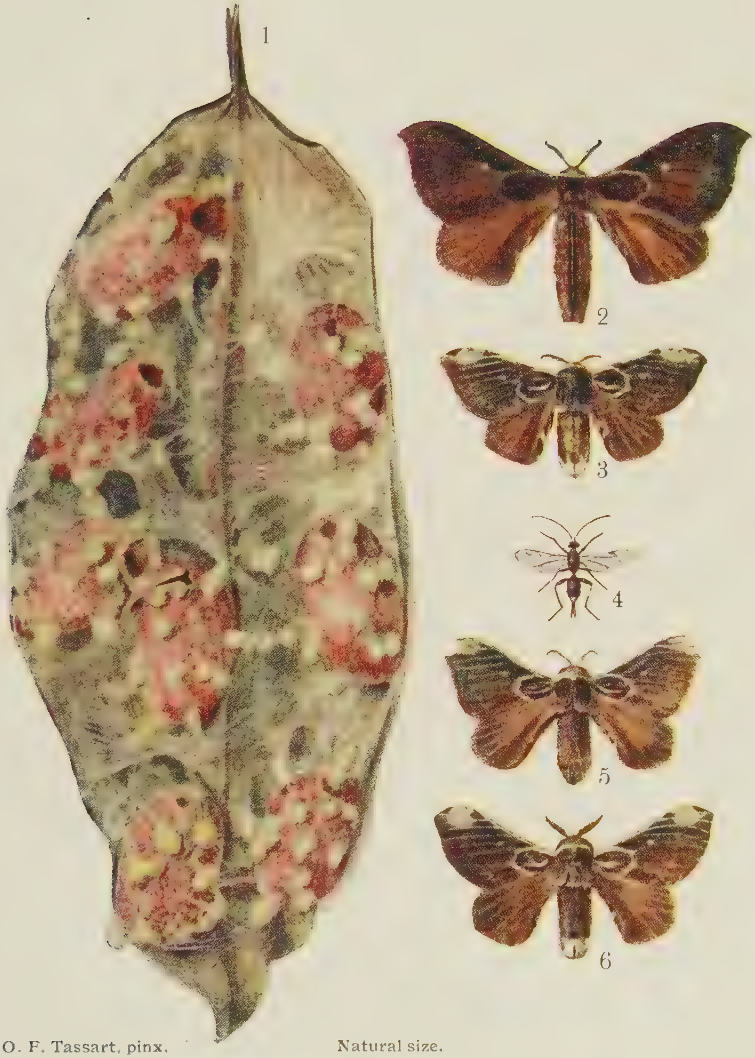
The most remarkable method of producing the same effect was observed by Mr. E. Ernest Green in the Tineid moth *Epicephala chalibacma*, Meyr., in Ceylon, and this may turn out to be the method of *Marmara*. The larva of *Epicephala* "after weaving a thin silken covering . . . rests for a few moments, and a convulsive movement of the posterior segments is noticeable. Very soon a globular pellet—apparently composed of dried bubbles—is voided whole. The caterpillar then turns round inside the cocoon, rapidly attaches the globule to the roof of the cocoon by a stout silken cord, bites a small hole close to the point of attachment, and pushes the globule and cord up through this aperture. The rent is then quickly repaired. This is followed by another short pause, the evacuation of a second pellet, and a repetition of the previous performance, the second pellet being placed at the opposite extremity of the cocoon, in consequence of the caterpillar having reversed its position in the cocoon. The same movements are continued, until the complete crest of globules is in position. . . . The number of pellets probably varies, but—in one cocoon—I have counted more than forty of these little objects" (*Ibid.*, **1912** : cvi–cix). It is interesting to note that these pellets are first produced inside the cocoon, and those of *Deilemera* and *Norasuma* outside a loose network which the larva subsequently enters and uses as its cocoon or within which it constructs a new one. The remarkable procedure of *Epicephala* has also been observed by Prof. T. Bainbrigge Fletcher and described by his Second Assistant, Y. Ramachandra Rao (*Ibid.*, **1913** : xxxviii–xl; see also **1912** : cix, cxxxviii).

Plate XIV.



O. F. Tassart, pinx. Natural size.

(1) Underside of Model, the Uraniid moth *Alcidis agathyrsus*, with orange patch on abdomen. (2) Underside of Mimic, *Papilio laglaizei*, with two orange marks forming a single patch over the abdomen when the hind wings come together (3).
Both model and mimic fly together in New Guinea.



O. F. Tassart, pinx. Natural size.

Underside of leaf with 8 cocoons of Bombycid moth *Norasuma kolga* (1). Yellow masses, spun on a loose net over the reddish cocoons, resemble cocoons of Braconid parasites. The female moth (2) and males (3, 5, 6) emerged from 4 red cocoons, an Ichneumonid (not Braconid) parasite (4) from another. W. A. Lamborn, Lagos District, 1912.

STUDIES OF NEW ZEALAND MAYFLY NYMPHS

By J. S. Phillips, M.C., M.A., B.Sc.

[Read 6th May, 1931.]

Plates XVI–XXIII.

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General.

Introductory.

Ephemeroptera or mayflies are insects which spend almost the whole of their life-cycle as aquatic nymphs, the winged stages lasting only a few days at most; they constitute a prominent item in the food of freshwater fish, notably trout, and such economic importance as they possess lies largely in this direction.

Little work has been done on this order in New Zealand, particularly on the nymphs.

Hudson (1) has published a short account of a number of mayflies. Hutton (2) gives a few brief notes on some of our species and includes a very complete generic key to the adults. In 1898 Lillie (3) described two species in rather more detail. The only mayfly nymph which has been at all adequately described is that of the rare *Oniscigaster wakefieldi* by Eaton (4) over forty years ago, who also wrote masterly accounts of a number of imagines and sub-imagines (4 and 5), though the only specimens available to him were either dried or in alcohol. Of recent years, Tillyard (6) has described two new species, but only in certain of the winged stages.

It is evident that there are big gaps in our knowledge of New Zealand mayflies, and, as a preliminary, it is necessary to supply descriptions of the undescribed stages of Ephemeroptera already named and keys for the identification of the various families and genera.

Consequently, I have embodied in this paper a key to the families and genera of New Zealand mayfly nymphs and short descriptions of the genera, showing their nymphal characters.

The accompanying key groups the Ephemeroptera into the three families recognised by Tillyard (7).

The generic key to nymphs has been drawn up so as to correlate their distinguishing features with those of the adults.

For this reason and because New Zealand mayfly nymphs possess structural features of their own, it has unfortunately been impossible to use the nymphal classification of either Needham (8 and 9) or Lestage (10).

It is usual to classify Ephemerid nymphs as *diggers*, *swimmers* and *crawlers*, and the three families in this country may fairly be considered in this aspect, though, among the SIPHLONURIDAE, *Coloburiscus humeralis* is a poor swimmer, and the term "crawling" is perhaps barely adequate to cover the diverse movements of all the LEPTOPHLEBIIDAE.

The structure of mayfly nymphs is described, so far as it affects New Zealand species, and their origin, affinities and distributions are discussed. Mention is made of their enemies and of the condition affecting their environment.

This paper is only concerned with the nymph proper, that is to say, the completely developed aquatic stage. The earlier or "larvule" stage, immediately after the emergence from the egg, when the insect is microscopic and devoid of many of the features which it possesses as a true nymph, is outside the scope of this work.

Papers dealing with all stages of the New Zealand Mayflies appear elsewhere (26 and 27).

Notes on Terminology.

In the following descriptions I have used certain terms that may not be in accord with those applied to similar parts of mayfly nymphs by writers in other countries.

To avoid any possible misunderstanding, the terms, together with the sense in which they are used, are as follows :—

PROSTHECA applied to the small finger-like process on the mandible, proximal to the inner canine. This term is used by Lestage and Imms. The prostheca is the *endopodite* of Eaton and the *lacinia* of American writers.

SUPERLINGUAE applied to the lateral lobes of the hypopharynx. Imms uses this term. American writers use the expression *lateral lobes*, Lestage *pièces laterales*, and Eaton calls them *paraglossae*.

GLOSSAE and PARAGLOSSAE applied to the internal and external paired lobes, which occur on the labium and are appended anteriorly to the mentum.

These terms are used by Imms and also by American writers on mayfly nymphs. Lestage, however, calls them *lobes internes* and *lobes externes*, and Eaton refers to them as the lobes of the *labium*.

LEGS. The terms *anterior* and *posterior*, *dorsal* and *ventral* are used in the same sense as they are used anatomically, irrespective of the actual position of the portion of the limb visible.

Thus the femur, tibia and tarsus of the limb of a mayfly nymph may be held with the *anterior* surfaces turned over so that they appear *dorsal*—as is very frequently the case—and may be figured so; nevertheless these surfaces will be described as *anterior surfaces*; the real *dorsal* surface will be described as such in the text, but in the case instanced will appear in the specimen—and probably the illustrations—as turned over so that it faces *posteriorly*.

Origin.

According to Tillyard (7), we owe our mayflies to a fauna which came from Antarctica in the Cretaceous Period. At this time there was a land mass over a considerable part of what is now the southern Pacific Ocean. ". . . While Western Australia was separated off, Eastern Australia extended over the Tasman Sea to include Tasmania, New Zealand, New Caledonia and even the Fiji Islands, and there was also a broad extension southwards, giving, at any rate for a time, a connection with Antarctica. This connection affected Eastern Australia and New Zealand about equally and supplied both with a number of types of cold climate and aquatic insects which form a very distinct element at the present day and are chiefly confined to New Zealand, Tasmania and the mountains of Eastern Australia. The chief representatives of this fauna are the whole of the mayflies except the BAETIDAE. . . ." (Tillyard).

The BAETIDAE, which are found in Australia but not, so far, in New Zealand, probably did not reach the former country until after New Zealand became separated from it.

The genera, which are found in this country, are mostly represented in Australia too, but never by the same species. Where the genera are unrepresented, there are genera of similar type.

Thus, in the family EPHEMERIDAE, there is, according to Tillyard (7), a nymph resembling *Ichthybotus* in New South Wales. The same authority states that our two genera of the family LEPTOPHLEBIIDAE, viz. *Atalophlebia* and *Deleatidium*, are represented in Australia.

Finally, among the SIPHLONURIDAE there are species of *Coloburiscus* in Victoria and New South Wales, and in the latter State there are mayflies very closely akin to *Ameletus*. *Oniscigaster* is not found, but in Tasmania and New South Wales there are species of a genus, *Tasmanophlebia*, Tillyard, which would appear to partake of some of the characters of both *Oniscigaster* and *Ameletus*.

So far as my information goes, no nymphs of a similar type to *Ameletopsis* * have been found in Australia. Did this remarkable mayfly spread to New Zealand with the other species, or is it possible that it originated from other sources? As yet, only the fringe of Ephemerology has been touched in this part of the world; further exploration may clarify the origin and position of this genus.

Distribution.

The fact that New Zealand is over 1200 miles from the nearest land mass has resulted in the evolution of a fauna different from that of the rest of the world.

Ephemeroptera are insects so incapable of surviving, for any appreciable period of time, when removed from their habitat, that it is impossible for individuals of species from outside to migrate here; nor, indeed, could any exotic species be accidentally introduced here in the winged stages—*e.g.* by lodgment on the structure of a ship at Sydney—as they do not live long enough.*

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* After this paper was written, I received a letter from Dr. Tillyard, dated Nov. 25th, 1930, stating that he had found a single nymphal specimen of an *Ameletopsis* sp. in the Cotter River, Australia. This nymph was almost exactly like that of *A. perscitus*, except that the cerci had no external fringe-hairs, but only internal ones.

All New Zealand species, therefore, are indigenous, and, as far as is known at present, are confined in their distribution to this country.

The narrowness of a land which, though extending through thirteen degrees of latitude, has no place more than seventy miles from the sea, has made the climate a remarkably equable one, and the temperature of the streams and rivers is not subject to marked seasonal changes.

Because of the hilly nature of the terrain in most parts of both Islands, the prevailing type of stream is rapid—and therefore well-oxygenated—and has a rough bed, usually of rock, boulders or shingle.

The annual rainfall is abundant, only falling short of twenty inches in a small area in the South Island and exceeding two hundred inches in parts of the West Coast. In the North Island, it is more uniform, as the annual rainfall ranges from forty to seventy inches in approximately eighty-seven per cent. of its area (22).

The consequence of so plentiful a precipitation on this hilly country is that there are innumerable streams and rivers and a large number of lakes; in fact, few countries can boast so large a mileage of fresh-waters in proportion to their area.

All these factors combine to produce an environment which is a singularly favourable habitat for Ephemeroptera, and naturally those species predominate which are most suited to the prevalent conditions, *i.e.* rapid mountain streams. There is, consequently, a large proportion of species of LEPTOPHLEBIIDAE and SIPHLONURIDAE and very few EPHEMERIDAE.

Little is known of the distribution of Ephemerid species in this country, except in the more settled areas.

Both the warm, sparsely-inhabited districts in the north of North Auckland and the wild hilly country of the Cold Lakes region in the south-west of the South Island are unknown territory, as far as mayflies are concerned, and there are probably many new species waiting to be discovered in such parts.

Nothing is known of the altitudinal range of the different species and a research into their zonation in the Southern Alps, for instance, on similar lines to the work carried out in the Rockies by Dodds and Hisaw (15), would be of immense interest and of no little value.

Such scanty information as we possess, at present, may be summarised as follows :—

The EPHEMERIDAE occur in the slower-flowing waters. Of the species of this family, *Ichthybotus hudsoni* is found in sandy patches of streams in the Wellington and Hawkes Bay districts and *I. bicolor* among rubble in the Nelson district.

Species of the SIPHLONURIDAE are found mainly in cold, well-aerated waters. *Coloburiscus* occurs in rapid waters in the Wellington, Hawkes Bay, Taupo, Nelson, Canterbury, Otago and Southland districts. *Oniscigaster* spp. live in well-bushed, cool, moderately-rapid streams among rock pools, boulders and shingle in the Wellington, Hawkes Bay, Nelson and Canterbury districts. *Ameletopsis* has been found in slow and moderately-flowing parts of streams in the Wellington and Hawkes Bay districts of the North Island.

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* This explains the absence of mayflies from all true "oceanic" islands, and the presence of any species of Ephemeroptera might almost be taken as proof that an island is not actually of the "oceanic" type.

Ameletus spp. are found in pools and in moderately-flowing rivers in the North Auckland, Taupo, Hawkes Bay, Wellington, Nelson and Canterbury districts.

Species of both genera of LEPTOPHLEBIIDAE are very abundant, according to Tillyard, all over New Zealand. In North Auckland I found the nymph of an *Atalophlebia* species, which I have not found further south. *Atalophlebia* appears to be the dominant genus in this district, whereas further south, *i.e.* throughout the greater part of the North Island, *Deleatidium* spp. would seem to predominate.

Unless otherwise stated, the data of distribution are from personal experience, either by visits to different places or from examination of trout stomachs sent from various parts of the country.

The accompanying map (Pl. XXIII) shows the position of the various districts.

As shown elsewhere (25), the mayfly is a most useful " indicator-organism," and a knowledge of the different species is, accordingly, a useful guide to anglers.

Enemies.

The chief enemy of mayflies in New Zealand is Man. His influence is entirely an indirect one, but is nevertheless very deadly.

By felling the bush near the water-courses he has altered the conditions in the streams, so that the beds dry up during the summer and nymphs and egg-masses become dessicated and die. Maimed insects are also occasionally found after freshets (due to the great increase in the rapidity of " run-off " from cleared land), in which they have been pounded by stones or other current-borne debris. A further result of felling has been the removal of shelter for the winged stages, and where transformation from the nymph takes place out of the water and the sub-imaginal stage is of long duration, *i.e.* among the SIPHLONURIDAE, this increased exposure has left the insects an easy prey to birds.

Among birds, the chief predators are the Pied Fantail (*Rhipidura flabellifera*), the Groundlark (*Austranthus novaeseelandiae*) and the Chaffinch (*Fringilla caelebs*), the first two being natives, the last being introduced by man.

An even more deadly predator is the introduced trout (both brown and rainbow varieties). As I have shown elsewhere (23), mayflies form nine per cent. numerically of the food of trout in the Wellington district. Tillyard (24) found that various Siphlonurids had been practically exterminated by the trout in various parts of the country.

The stomach of an Atlantic Salmon, sent to me from the Waiau river, Southland, contained between two and three hundred nymphs of *Coloburiscus humeralis*, showing that another introduced fish was levying toll on the mayfly.

Native fish, especially the bully (*Gobiomorphus gobioides*) were found (23) to eat mayfly nymphs, as do the nymphs of some stone-flies, the larvae of aquatic, carnivorous beetles and of the " creeper " (*Archichauliodes dubitatus*). I have found small mayfly nymphs helplessly ensnared in the traps of web-spinning caddis larvae.

Species of LEPTOPHLEBIIDAE are particularly susceptible to attack by Nematodes, and a large percentage of the individuals of this family are parasitised.

EXTERNAL ANATOMY.

New Zealand mayfly nymphs vary considerably in appearance according to genus. Their general shape is campodeiform. The longitudinal axis of the head is usually in line with that of the body, which in that case is more or less flattened dorso-ventrally, the eyes being placed dorsally; but, in all species of the family Siphlonuridae except *Ameletopsis*, the axes of the head and body are at right angles, and the body is not flattened dorso-ventrally, the eyes then being placed laterally.

The Head.

The head may be comparatively small as in *Ichthybotus*, or large as in *Ameletopsis*. In other species it is intermediate in sizes between these two, in comparison with the body.

The dorsal region of the head is formed of three pieces—a medio-anterior portion, the clypeo-frons, which bears the antennae and the median ocellus, and two symmetrical posterior parts, which comprise the epicranium; each of these two parts bears a compound eye and one of the lateral ocelli. These three parts are separated from each other by the Y-shaped epicranial suture (shown in the head of *Ichthybotus hudsoni*, Pl. XX, fig. 4).

The compound eyes, which are of the eucone type, are placed dorsally (Pl. XX, fig. 4, Pl. XXI, fig. 1, Pl. XIX, fig. 1), except in most of the Siphlonuridae (not *Ameletopsis*), where they are laterally placed; they are composed of a large number of ommatidia. The eyes seem to occupy a considerable part of the head, especially in such genera as *Ameletus* and *Oniscigaster*, where the head is small and its axis is placed at right angles to that of the body. In the males of a number of genera (*Atalophlebia*, *Deleatidium* and *Ameletopsis*), the eyes are larger than those of the female. In these three genera, the male has turban eyes, *i.e.* each eye is composed of an upper and inner portion and a lower and outer one: the upper portions have appreciably larger facets than the lower ones and are, moreover, usually of a lighter colour; the colour of the lower parts is similar to that of the eyes of the female of the species.

In addition to the compound eyes, there are three small ocelli (Pl. XX, fig. 4, Pl. XXI, fig. 1, Pl. XIX, fig. 1), two being placed laterally—each about midway between the eye and the antennal pit—and the third placed medianly and slightly posterior to a line joining the antennal pits.

The antennae are filiform and multiarticulate, being about as long as the head and thorax combined, considerably shorter in *Ameletus* and *Oniscigaster*.

The Mouth-parts.

These are very highly developed and show marked differences in the various genera.

(1) *The Labrum* is a median unpaired appendage, placed antero-medianly of the clypeus, with which it articulates. It is connected to the clypeo-frons by pairs of muscular attachments—a median pair, which is abductory in function, and a pair of lateral attachments, which connect at the latero-posterior angles and are adductory in function. The labrum appears to be used mainly as a scraper, but it also pushes food into the mouth from above or in front. The anterior edge is always armed with hairs or spines, except in that of *Ameletopsis perscitus* (Pl. XIX, fig. 2). This edge may be straight as in *Coloburiscus humeralis* (Pl. XVI, fig. 17), or convex as in *Ameletopsis perscitus* (Pl. XVI, fig. 20), or concave as in *Atalophlebia versicolor* (Pl. XVI, fig. 22); it may have a deep notch as in *Deleatidium* spp. (Pl. XVI, figs. 14 and 15), or a number of teeth as in *Atalophlebia cruentata* (Pl. XVI, fig. 21), or a slight bay as

in *Ichthybotus hudsoni* (Pl. XVI, fig. 18). The proportion of breadth to length also varies to some degree. Both surfaces of the labrum are covered with hairs or spines, particularly on the anterior half (except in *Ameletopsis perscitus*, which is hairless).

In the LEPTOPHLEBIIDAE there is an inconspicuous tongue-shaped patch of small hairs, placed medio-posteriorly—though slightly to one side—on the ventral surface.

(2) *The Mandibles* are paired appendages which move laterally. Usually, each is armed distally with two sets of teeth—the canines and the molars; the latter set are placed differently in each mandible, being placed dorso-anteriorly on the inner margin of the right mandible and ventrally on the inner part of the anterior margin of the left mandible, but when the mandibles are closed, the molars fit into each other dorso-ventrally. They are used for grinding; each consists of a number of parallel ridges—about ten—which rub together and triturate the food. These ridges are usually serrated and armed with short, stiff bristles. The canines are used for tearing; they consist of an outer and an inner canine, each of which is subdivided into smaller teeth—usually three; interior to the canines is a minute, jointless, mobile, finger-like process, the prostheca, and attached to its base is a small bunch of hairs of about its own length. The exterior edge of the mandible always bears a fringe of hairs.

This type of mandible is the normal one and occurs in all the LEPTOPHLEBIIDAE (Pl. XVIII, fig. 6), and in *Coloburiscus* and *Oniscigaster* (Pl. XVII, fig. 6) among the SIPHLONURIDAE. In *Ameletus* (Pl. XXII, fig. 6) the canines have coalesced; in *Ameletopsis* (Pl. XIX, fig. 3) the molar surface has almost disappeared and the canines have developed very strongly and become a formidable weapon; the only other mayfly with canines at all like this is Eaton's unidentified nymph from Chili.

In the EPHEMERIDAE (Pl. XX, fig. 6) the salient feature is the development of part of each mandible into an enormous fossorial tusk, pointed at the end and armed extensively with short, stout spines and a fringe of long hairs. This tusk, which is used for digging burrows, has been called a canine by some writers, but it is not one, for the real canines, somewhat modified in form, are there too, as are the molars.

(3) *The Maxillae* are also paired appendages, working laterally. They consist normally of a basal part—the cardo, a stipes, which merges distally into a fused galea-lacinia, and a palp, the palpifer of which may or may not be fused with the basal segment.

In the EPHEMERIDAE (Pl. XX, fig. 7) the palp is three-segmented and large, and the galea-lacinia is greatly reduced.

Among the SIPHLONURIDAE, *Coloburiscus* (Pl. XXI, fig. 3) has a very large two-segmented palp, heavily fringed with hairs, and a short galea-lacinia [Murphy (12) suggests—with reference to an American species with a similar palp and rapid-water habitat—that this fringe acts as a diatom strainer], *Oniscigaster* (Pl. XVII, fig. 7) has a three-segmented palp with a galea-lacinia of about equal length; in *Ameletus* (Pl. XXII, fig. 8) the proportions are somewhat similar, but the terminal joint of the palp is shorter, more rounded apically and armed with curious sensillae, and the suture between galea and lacinia is apparent—which is exceptional in local species. *Ameletopsis* (Pl. XIX, fig. 5) shows extraordinarily aberrant features—again, only comparable to Eaton's nameless Chilian nymph. The palp is much reduced in size and multiarticulate, the galea-lacinia ends in a number of formidable, long, spine-like teeth; together with the mandibles, these maxillae form an effective, carnivorous armament.

The maxillae of species of LEPTOPHLEBIIDAE (Pl. XVIII, fig. 4) are very uniform. The galea-lacinia ends in a broad brush of brown hairs, which is used for brushing food into the mouth-cavity and possibly as a diatom strainer of passing water. Hidden by the brush of hairs is half a row of pectinate rakes (Pl. XVIII, fig. 10), which are inserted, starting from the interior corner, along the margin. What are the functions of these curious rakes? Do they comb the food from stones or perhaps from the other trophi? I have noticed a frequent brushing action between the forelegs (which are usually very spinose) and the maxillae, and it is just possible that the combs are used to convey diatoms and other matter from the forelegs. The palp is three-segmented and projects somewhat beyond the galea-lacinia.

(4) *The Hypopharynx* is an unpaired median structure—possibly a fusion of what were originally two-paired structures—which fits dorsally over the labium. It is a sort of trilobed tongue, usually covered with long hairs anteriorly, and consists of a median and two lateral pieces; the latter are called the superlinguae.

Sometimes the median piece is much reduced as in *Ichthybotus* (Pl. XX, fig. 1), sometimes it is about equal in size to each of the two lateral parts as in *Oniscigaster* (Pl. XVII, fig. 2), and sometimes considerably larger as in *Ameletopsis* (Pl. XIX, fig. 4, where it is shown superimposed on the labium). The superlinguae show their maximum development in the LEPTOPHLEBIIDAE (Pl. XVIII, fig. 9).

(5) *The Labium* or lower lip is composed of a pair of lateral appendages fused together. It sweeps food from below or behind (depending on the angle of the head axis to that of the body) into the mouth-cavity. Situated proximally on this mouth-part are the mentum and submentum, which are often incompletely differentiated. Attached to the mentum laterally are the labial palps, which are somewhat variable in form. In *Ichthybotus* (Pl. XX, fig. 5) they are two-segmented, the distal segment being large, flattened, falcate and very hairy; in *Coloburiscus* (Pl. XXI, fig. 6) these characters are even more pronounced. According to Morgan (18), this type of palp is a characteristic of the nymphs, living in swift currents, which use the blade-like distal segments as scrapers upon stones covered with algae and the hair as a plankton basket. This would certainly apply to *Coloburiscus*, but *Ichthybotus* is a slow-water form. The most characteristic, three-segmented palps are shown by *Oniscigaster* (Pl. XVII, fig. 8), *Ameletus* (Pl. XXII, fig. 7) and *Atalophlebia* (Pl. XVIII, fig. 7). *Ameletopsis* (Pl. XIX, fig. 4) again shows an extraordinary form, the palp being long, thin and multiarticulate. Probably it was originally bi-segmented, the basal joint remaining unchanged, the distal one becoming subdivided into a number of smaller joints and becoming narrowed and elongated in the process.

The distal attachments of the mentum are a pair of inner segments (the glossae) and an outer pair (the paraglossae). These may be considered as the laciniae and galeae respectively of the second maxillae. They are always covered with hairs or spines, particularly in the anterior parts, and in *Ameletus* (Pl. XXII, fig. 7) they bear curious sensillae (Pl. XXII, fig. 9), as do the palps; possibly these are gustatory in function. Pls. XVII, fig. 8; XVIII, fig. 7; XIX, fig. 4; XXI, fig. 6; XXII, fig. 7 show various types of these parts of the labium.

The Thorax.

This part of the body contains three segments of about equal width but varying length. The prothorax is always short, the mesothorax considerably longer and the metathorax about as long as the prothorax. This latter segment is well differentiated, but the meso- and metathorax are completely covered dorsally by the wing-pads,* so that their dividing line cannot be seen. The wing-pads of the hind-wings, which spring from the metathorax, are concealed by those of the fore-wings, which are mesothoracic in origin and which also cover some of the anterior abdominal segments in older nymphs.

Attached to each thoracic segment is a pair of legs, composed of coxa, trochanter, femur, tibia and tarsus. The femur is by far the largest part of the leg, next is the tibia and after that the tarsus; both coxa and trochanter are very small (these two parts are not shown in the legs figured). The tarsus, like the other parts of the leg, is composed of a single segment (adults have multi-segmented tarsi) and ends in a claw.

The legs of different species of nymphs indicate by their appearance the kind of habitat of the species. Thus, the legs of *Ichthybotus hudsoni* (Pl. XX, fig. 11) show how completely the burrowing habits of that nymph are in accordance, with the development of its legs, and it is only necessary to see the speed with which this insect buries itself to realise their efficiency. Compare these with the poorly-developed, almost bare legs of *Ameletopsis* (Pl. XIX, fig. 6) and *Oniscigaster* (Pl. XVII, fig. 4), the nymphs of which are of the swimming type but still crawl a little, and then with the still further reduced legs of *Ameletus* (Pl. XXII, fig. 2), which is solely a swimmer.

Coloburiscus (Pl. XXI, fig. 2) shows an interesting modification. This nymph lives in the rapids, and in its case the legs are heavily spined to help it maintain its foothold; moreover, the fore-legs are thickly fringed, and, when held in the characteristic position, form with the hair fringes of the mouth-parts a plankton trap, with which this nymph strains the rapid-flowing water of its habitat.

Finally, the LEPTOPHLEBIIDAE (Pl. XVIII, fig. 2) have their femora flattened and covered with spines, and also have spines on the tibiae and tarsi; these features, as well as the serrated tarsal claws, help them to retain their hold on the surfaces of stones and in the crevices, even in the swifter streams. Their legs are longer and far more efficient than those of the SIPHLONURIDAE, and they not only help them to hang on in rapid water but also to travel with great agility forwards, backwards and even sideways. If a submerged stone be picked up from the river and the lower surface inspected, as soon as the stone has been turned over the Leptophlebiid nymphs will dodge like lightning round to the other, unexposed side or lodge themselves in a handy crevice.

The Abdomen.

The abdomen, which is by far the largest part of the body, is made up of ten segments, varying slightly in length and width, but always becoming narrower posteriorly. The first segment is fused with the metathorax. Usually the segments broaden slightly from the front until the middle of the abdomen is reached and then narrow less gradually to the last segment. The ninth segment is usually longer than the others, the tenth being very much shorter and narrower. In most species, the latero-posterior angles of segments (particularly those of the posterior segments) are produced backwards as sharp teeth; this is very marked in *Coloburiscus* (Pl. XXI, fig. 1) and *Atalophlebia* (Pl. XVIII, fig. 1).

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* The wing-pads contain the larval wings, and it was upon a study of the tracheation of these structures, in local species of the family SIPHLONURIDAE, that Tillyard based his work concerning the wing-venation of this order (19).

The abdomen may be slightly flattened dorso-ventrally as in *Ameletopsis*, decidedly flattened as in *Atalophlebia*, or pronouncedly flattened as in *Deleatidium*. In the swimming nymphs it is cylindrical, tapering posteriorly. *Ameletus* has a torpedo-shaped abdomen, and *Oniscigaster*, though considerably broader laterally than dorso-ventrally, also pertains to the "stream-line" type.

The tenth segment bears three caudal setae apically, each consisting of a large number of small, cylindrical segments. Tillyard (7) calls the median seta the appendix dorsalis, but, for the sake of convenience, the term caudal seta will be applied, in this paper, to all three of the caudal filaments.

In all cases the two lateral setae are of the same length; in the EPHEMERIDAE and LEPTOPHLEBIIDAE the median seta is very slightly longer, in the SIPHLONURIDAE very slightly shorter than the others. In *Coloburiscus humeralis* (Pl. XXI, fig. 1), which belongs to the last-named family, the median seta has been very greatly reduced and is now rudimentary and made up of a few segments only. It is interesting to note that an undescribed Australian species * of this genus has the median seta normal. Doubtless, in the local species, the seta has become partly atrophied, as it is useless in the habitat that this nymph has adopted.

In the EPHEMERIDAE the caudal setae are short and haired throughout on both sides. Among the SIPHLONURIDAE these appendages are nearly always used—interlocked by their thick fringes—as an oar, and they propel the insect through the water by strong dorso-ventral strokes. The form of seta most favourable to propulsion is seen to be a short, thickly-fringed type (*Ameletus* and *Oniscigaster*). In both these genera, the median seta is thickly fringed on both sides, the outer ones on the inner sides only (Pl. XXII, fig. 4). In *Ameletopsis* all three setae are fringed on both sides. *Coloburiscus* is again an exception; it is a poor swimmer and its setae are not fringed at all, but have a whorl of short, weak hairs at the segmental junctions (not shown in Pl. XXI, fig. 1, as they are too small). This type of seta is also found universally among the LEPTOPHLEBIIDAE. Most of the species of this family have long thin setae, which seem to act as secondary balancing organs and as a mild brake, when spread out, as they settle on a surface after a short—and usually involuntary—swim.

The Gills.

On each of the first seven segments of the abdomen there is a pair of gills. These interesting structures, which do not appear until several days after hatching—the new-born Ephemerid breathes cutaneously—are exceedingly diversiform in the different genera.

They were, originally, incorrectly believed to be homologous with wings, but Heymons [(20) and elsewhere] has shown that they arise as laterally-placed hypodermal thickenings and are not tergal outgrowths. Borner (21) has written a very interesting and intricately-reasoned paper, on the origin of these appendages, from a morphological standpoint.

In all the New Zealand species these organs are paired and occur, placed posteriorly, on each side of the segments. Secondary gills do not occur on either the thorax or the maxillae, as occasionally happens in species from other countries.

The gills are either foliaceous or composed of a number of filaments. Usually they attain their maximum development in the middle pairs, whilst either the anterior or the posterior gills, or sometimes both, are less strongly developed or even abortive.

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* Specimens of this undescribed species were kindly sent me by Dr. Tillyard, so that I might compare them with N.Z. species.

In *Ichthybotus* the anterior gills are aborted and are each in the form of a microscopic bifid lash (Pl. XX, fig. 2), whilst in each of the other pairs each gill is double and resembles a pair of feathers (Pl. XX, fig. 3), the "rachis" of the feather containing the trachea and the long, thin "barbs"—the gill filaments—each contain a tracheal branch. These filaments are minutely serrated on each edge, and from the apex of each serration, a small spine projects forwards and outwards. The gills are held upright over the dorsum. They are held similarly in *Coloburiscus humeralis*, a nymph with very differently shaped gills, which increase in size posteriorly (Pl. XXI, fig. 1); this increase is noticeable in the outer fork of each gill only, but the entire gill is smaller in the anterior pair. Each gill (Pl. XXI, fig. 5) is pedunculate and consists of a divergent fork, united in the basal half by a thin lamella. It is armed with numerous short spines, which occur mainly round the edges and towards the distal part. These spines are jointed at the base and can be made to lie flat along the gill surface, but spring up when pressure is removed. It is probable that the purpose of this stout but elastic armament is to protect the gill from damage by the current-borne debris, which abounds in the swift habitat of this nymph. Under the surface of each lamella lies an extensive ramification of tracheoles, and a tracheal branch runs along the middle of each of the forks.

It is interesting to note that the gills of the allied undescribed Australian species mentioned above, p. 408, have tufts of gill filaments at the base of the gills.

Oniscigaster is the only other New Zealand genus in which the gills are held dorsally. Pl. XVI, fig. 2, shows a typical gill. Eaton [(4) Pl. LI] illustrates these elaborate gills very beautifully but omits the posterior gill; they are diversiform and become smaller posteriorly, the last gill being microscopic and probably functionless. They are either green, marbled with white, or red, marbled with white, and are agitated slowly. The rhythm of this movement combined with the beauty of the gills makes it a delight to watch.

The gills of all the other genera are held laterally. Among the SIPHLONURIDAE there remain *Ameletus* and *Ameletopsis*. Both have single lamellate gills, ovate in outline, with rounded apices. There is a central trachea and many branches, frequently much ramified, in each gill. The gills of *Ameletus* (Pl. XXII, fig. 3) decrease in size both anteriorly and posteriorly; their edges are finely toothed in the upper distal portions and bear minute hairs all round, except in a small, upper proximal portion. Below the main tracheal branch, a thick, chitinised, curved band runs longitudinally throughout the gill, acting as a brace.

In *Ameletopsis* (Pl. XIX, fig. 8) the edges are entire and there is no brace.

The LEPTOPHLEBIIDAE show two types of gills, double and single. In *Atalophlebia* the gills are double and become smaller and narrower posteriorly, the seventh gill often being aborted. They are either each in the form of a pair of ovate-acuminate lamellae, e.g. *A. versicolor* (Pl. XVIII, fig. 8), or lanceolate-acuminate. In most cases they have a prominent central trachea, which is pinnately branched, but in *A. nodularis*, where the gills are lanceolate, the main tracheae are unbranched.

Finally, the genus *Deleatidium* has single, lamelliform gills, those of the second to seventh pairs being usually ovate-acuminate as in *D. vernale* (Pl. XVI, fig. 7), but in one case (*D. myzobranchia*) sub-rotund (Pl. XVI, fig. 6). In all these species, the gills become smaller posteriorly and the shape of the first gill is similar to the outline of a kidney and therefore different from that of the others (Pl. XVIII, figs. 11 and 12). All the gills have each a main trachea with pinnate branching, sometimes much ramified.

In *D. myzobranchia* the gills frequently appear to be held in such a position that they act as suckers and help to hold the insect to the substratum in swift waters.

It is interesting to speculate as to whether the changes which are occurring in this country—due to comparatively recent settlement by Europeans—will induce the mayfly to evolve new adaptations to meet the altered conditions. Thus, *Oniscigaster* has become comparatively rare, for reasons indicated elsewhere in this paper, and it is probable that it must evolve protective measures to meet the new conditions or become extinct.

The clearing of bush from the stream banks and catchment areas has altered many miles of our freshwaters; their beds often change and frequently become dry in midsummer; much of their course is now strewn with pebbles, which move downstream with each severe freshet. These altered conditions affect the mayfly and may influence it, in many ways, in due course.

Dr. Tillyard recently sent me specimens of an undescribed Siphlonurid from Australia. This nymph showed affinities with both *Ameletus* and *Oniscigaster.* The gills were reduced to four pairs, of which those of the first pair were large and thickened, forming an operculum to protect the three posterior gills. It occurred to me that such an evolution may possibly be due to recurrent dry seasons and be a xerophytic adaptation.

In such pebble beds as have become temporarily dry, in this country, mayfly nymphs may often be found a few inches below the surface of the bed, where it is generally cool and damp.

CLASSIFICATION.

Key to Families and Genera of New Zealand Ephemeroptera.

NYMPHS.

A. MANDIBLES WITH TUSK-LIKE EXTENSION, PROTRUDING IN FRONT OF HEAD. (Plate XVI, fig. 9) . . . . EPHEMERIDAE.

With six pairs of gills, visible to the unaided eye: these are feathery and lie on the dorsum (on 2nd to 7th abdominal segments). (Plate XVI, fig. 1.)

(NOTE.—There is another pair on the first abdominal segment, but it is microscopic).

B. MANDIBLES SHORT, NOT EXTENDING IN FRONT OF HEAD.

I. **Caudal setae densely haired throughout their length.*

†*Tarsal claws not toothed underneath* (Plate XVI, fig. 12) SIPHLONURIDAE.

With seven pairs of gills.

1. *Gills held upright over the dorsum.*

(i) Gills forked and with numerous spines (Plate XVI, fig. 3). *Coloburiscus*, Eaton.

(Median caudal seta very short).

(ii) Gills lamellate and recumbent on dorsum (Plate XVI, fig. 2). . . . . *Oniscigaster*, McLachlan.

(7th pair microscopic).

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* Except *Coloburiscus.*

† The claws of *Ameletus ornatus* have a number of very minute serrations underneath, but these are very much smaller than those of a Leptophlebiid claw.

2. *Gills held extended laterally: lamellate* (Plate XVI, figs. 4 & 5).
    - (i) Head small (Plate XVI, fig. 10): palps three-jointed: outer caudal setae haired internally . . *Ameletus*, Eaton.
    - (ii) Head large and skull-like (Plate XVI, fig. 11): palps many-jointed: outer setae haired on both sides *Ameletopsis*, gen. n.

II. *Caudal setae with whorls of a few thin, short hairs at joints. Tarsal claws toothed underneath* (Plate XVI, fig. 12) . LEPTOPHLEBIIDAE.
- A. *Gills double* (Plate XVI, fig. 8) . . . . . *Atalophlebia*, Eaton.
- B. *Gills single* (Plate XVI, figs. 6 & 7) . . . *Deleatidium*, Eaton.

Family EPHEMERIDAE.

This family is identical with Lestage's (10) family EPHEMERIDAE and Needham's (8) sub-family EPHEMERINAE.

In New Zealand the "diggers" are represented by only one genus, *Ichthybotus.* It very greatly resembles the type *Ephemera* of Eaton (4), having the characteristic digging tusk projecting in front of the head, the modified fore-legs which assist fossorial operations, and the double feathery gills which are held over the dorsum and keep aerated water circulating in the creature's burrow.

It differs from *Ephemera* in that the head does not narrow anteriorly; the tusks are shorter, broader and curve *inwards,* not outwards apically; the clypeus is not deeply incurved anteriorly; the setae are shorter in proportion to the length of body, and the labrum is wider in proportion to its length and has concave lateral margins.

Genus **Ichthybotus,** Eaton (1899).

Mandibles prolonged in front of the head in the form of tusks, which curve inwards apically. Maxillary palp of three segments; labial palp of two segments. Antennae long, filiform. Body elongated, tapering posteriorly, convex dorsally. Legs robust, densely haired: order of length, 3, 1, 2: anterior pair adapted for digging: claws untoothed. Six pairs of double feathery gills held upright over dorsum on the second to seventh abdominal segments and one minute, rudimentary pair, each gill in the form of a bifid lash, on the first abdominal segment. Caudal setae short, densely haired on both sides: median seta slightly longer than the others.

There are two species, *I. hudsoni* (McLachlan), which is well distributed throughout New Zealand and is described below, and *I. bicolor*, Tillyard, which occurs in certain parts of the northern districts of the South Island.

Of this second species, Dr. Tillyard writes in a recent letter. . . .

"This latter larva does not differ very much from the larva of the North Island species, *I. hudsoni*, but is smaller and darker in colour. The specimens which we found were in loose, coarse, mixed shingle and mud in the river bed, not actually tunnelling in clay, though the latter is the usual habit for the North Island species."

Until quite recently I had not had the opportunity of seeing this species, but on Jan. 23rd, 1930, I captured a single specimen in the Gowan river, Nelson Province. This nymph was fully-grown, but unfortunately it died before reaching my aquarium at Wellington. However, it was obviously almost ready to transform to the sub-imaginal stage, so that a dissection of the wing-pads proved it to be a nymph of *I. bicolor*. Whilst alive, the dorsal aspect of the head, the mandibular tusks and fore-legs all had a reddish tinge.

In the summer of 1929–30 I found similar nymphs in the North Island, not in burrows but among rock and rubble in George's Creek, a small tributary which feeds the headwaters of the Wainui-o-mata, about 15 miles east of Wellington.

Unfortunately I was unsuccessful in rearing them, as they met with an accident in the aquarium.

This suspected change of habitat from tunnels in sand or loose mud to living in loose rubble is most interesting, but requires further confirmation.

Incidentally, the opportunity is taken of pointing out that gills are present on the first *seven* abdominal segments, not on the first *six*, Hudson (1) having apparently mistaken the second abdominal segment for the first, which is fused with the metathorax and which bears very minute, reduced gills.

Moreover, the writer would like to submit the opinion that Lestage (10), in describing the family EPHEMERIDAE, was mistaken in regarding the mandibular tusk as a canine, for both outer and inner canines are present, in addition to the tusk, in our species, as indeed they are in American (see Murphy (12), text-fig. 1, p. 16) and European species (Eaton (4), plates, and Needham (13), plates).

A characteristic nymph of this family, *i.e.* a "digger," burrows in the sandy or muddy banks of streams below water-level. It swims with dorso-ventral, undulating movements of the body.

An Ephemerid nymph (*E. vulgata*) was described in some detail by Vayssière (16), and these are very similar.

There is one peculiarity in the structure of this nymph which is very puzzling. As I have seen no mention of it in descriptions of nymphs from other places, it may be a local characteristic. This is the presence of a few feathered hairs, among the normal type, on the legs of specimens of this genus; these hairs occur mainly along the edges. The only other nymph which has these curious hairs is *Atalophlebia cruentata*, an entirely unrelated species, and, in this case, they appear on the anterior pair of legs only.

A feathered hair is illustrated (Pl. XX, fig. 9), as are various other parts of the nymph of *Ichthybotus hudsoni*, a typical nymph of this family (Pl. XX, figs. 1 to 11).

It is unusual to find large swarms of a species of this family in New Zealand, as in many other countries, for in the swift streams with beds of rock, boulders or shingle, there are only occasional patches of sand or mud suitable for the tunnels of burrowing nymphs.

If a nymph of *I. hudsoni* is dug out of its tunnel it will bury itself in the nearest sandy patch, burrowing with its fore legs and mandibular tusks and digging itself in with remarkable rapidity.

When about to transform, nymphs in the writer's aquarium left their burrows and floated for some time, unmoving, on the surface of the water, rarely agitating their gills.

A quantity of air was noted under the skin of the thorax and of the anterior part of the abdomen.

The actual metamorphosis, which occurred as usual through a longitudinal rent in the dorsum of the thorax, was extraordinarily swift, in marked contrast to the long time (sometimes hours) spent on the surface waiting for the change. This protracted wait may have been due to the unnaturally still condition of the water present in the aquarium.

The winged stages appear in December, January and February, but, as nymphs of various sizes are seen at this time, it is likely that this fly has a two-year or even possibly a three-year life-cycle.

The wings of the sub-imago sometimes show curious variations from the normal type, and it is hoped to deal with this subject at a later date.

Family SIPHLONURIDAE.

The New Zealand genera, which this family contains, are of especial interest as they possess many uncommon features.

Tillyard (7) considers the members of this family to be very archaic types. At least one genus is also represented in Eastern Australia, and the others show affinities to some of the genera in that district or to those of Tasmania; but, so far as present-day investigations have disclosed, similar types have not been found elsewhere, and though two of our species still remain, for the present, in the genus *Ameletus*, it is practically certain that they do not really belong there.

Owing to various structural features of New Zealand Siphlonurids, it is impossible to adopt, in their entirety, the characters for the sub-family BAETINAE proposed by Needham (8), or those of Lestage's sub-family SIPHLONURINAE, with both of which this family (*i.e.* the SIPHLONURIDAE) corresponds to a considerable degree.

Needham in his classification (8) states :—". . . sub-family BAETINAE; a very heterogeneous series, only definable as lacking the characteristics of the other two" (*i.e.* sub-families EPHEMERINAE and HEPTAGENINAE) "and including five fairly distinct groups. . . ." (It should be pointed out that Needham's sub-families would correspond to present-day families, as his work was written before mayflies had been accorded ordinal rank.)

In spite of the wide range which his statement embraces and the small number of sub-family characteristics—

> "Mandibles without projecting tusk-like ramus.
> Gills not as in EPHEMERINAE.
> Eyes lateral : form of body various : claws smooth or toothed below"—

the fact that one genus (*Ameletopsis*) has the eyes placed dorsally would prevent our adopting this classification; moreover, the range of the BAETINAE is so wide that it would include the Australasian family LEPTOPHLEBIIDAE as well.

Lestage (10) is rather more detailed in his keys; for his family BAETIDAE he gives—

> "Branchies externes, dorsales ou latéro-abdominales, mais toujours visibles."
> "Mandibles très courtes sans aucun prolongement antécéphalique : pattes grêles ou dilatées mais inaptes à fouir; branchies jamais plumeuses :"
> "Yeux latéraux; corps peu ou pas aplati dorso-ventralement, généralement cylindrique."

and for the sub-family SIPHLONURINAE—

> "Ongles jamais plus longs que les tibias, parfois bifides . . .; parfois ongles simples et alors branchies simples, bi- ou monolamellaires, mais sans branchies auxiliaires, et les pattes faiblement ciliées."

Here again *Ameletopsis* does not conform to a number of these conditions. The body is rather pronouncedly flattened dorso-ventrally, the eyes are *dorsal*, the lateral tails are haired on *both* sides.

Neither could *Coloburiscus* be included here, for its legs are not thin and the first two pairs carry long fringes of hair; moreover, the gills are not lamellate and the tails have very short hairs in whorls on both sides.

I therefore assign the following nymphal characters to the family SIPHLONURIDAE—

Nymph of the swimming type; body usually somewhat cylindrical. Eyes generally lateral. Mandibles short, not extending in front of head. With seven pairs of single gills, inserted dorsally or latero-abdominally. Legs short. Claws seldom toothed underneath. Caudal setae *either* strongly fringed with long hair throughout, all three sub-equal in length and shorter than the body, *or* with very short hair in whorls, in which case the lateral setae are about equal in length to the body and the median one is very short.

Genus **Coloburiscus,** Eaton (1887).

Head convex dorsally and with fringe of hair anteriorly. Eyes lateral. Maxillary and labial palps two-segmented and greatly enlarged. Thorax very large and prominent. Anterior and middle pairs of legs with long fringe of hair anteriorly; order of length of legs 1, 3, 2. Claws not toothed. Latero-posterior angles of 3rd to 9th segments of abdomen projecting backwards as sharp teeth. Caudal setae with very short hairs in whorls at joints of segments; the outer setae about as long as the body; the middle one very short. With a pair of gills on each of the first seven abdominal segments, held upright over the dorsum. Each gill composed of a divergent fork with connective membrane basally and covered with spines.

Habitat in rapids and the fast-flowing parts of streams.

There is only one species, *C. humeralis* (Walker), which is widely distributed throughout New Zealand.

This is the unknown nymph mentioned and figured by Lillie (17); and Hudson (1) has a short description of it.

It lives among the rapids and swiftly-flowing portions of the streams and will not live in poorly-oxygenated water. Both Lillie and Hudson attempted to rear it, but were unsuccessful. Nevertheless, given an aquarium with a constant stream of well-aerated water running through it, the nymph can be kept for months quite successfully and will eventually transform into the subimaginal stage. As in all members of this family, the transformation does not take place from the surface of the water but from some solid support on to which the nymph crawls and leaves its cast nymphal skin.

This species is found attached to stones, rocks or boulders and among the vegetable debris which is often lodged among the boulders in rapids. Here, it will cling with remarkable tenacity despite the force of the current, helped doubtless by the many spines, with which its legs and the ventral surface of its abdomen are armed.

It is a poor swimmer, moving its legs in unison jerkily backwards and forwards, and there is at the same time a slight dorso-ventral movement of the tip of the abdomen; after a few spasmodic jerks, it often stops and curves the hinder part of its abdomen upwards and forwards.

The fringes of hair on its fore legs and mouth-parts (Pl. XXI, figs. 1 and 2) would seem to form a plankton straining apparatus, which enables it to secure food from the rapidly-passing water without undue exertion, while its peculiar gills—unlike those of other New Zealand mayfly nymphs—are held motionless, as it is unnecessary for the insect to move them to obtain fresh oxygen in the swift currents of its habitat.

No other species of this order in New Zealand has succeeded so well in adapting itself to torrential aquatic conditions, and consequently it is the predominant nymph of the rapids.

Metamorphosis to the sub-imaginal stage occurs at the end of spring and throughout the summer.

Illustrations of details of the structure of this nymph are included. (Pl. XXI, figs. 1 to 6.)

Dr. Tillyard kindly sent me specimens of an undescribed Australian nymph of this genus (see p. 408) in which it was interesting to note that the median caudal seta was as long as the others and that the gills had accessory tufts of fibrils at the base.

Genus **Oniscigaster,** McLachlan (1873).

Oniscoidal in form. Head small. Eyes lateral. Antennae short. Labial and maxillary palps, each of three segments. Thorax broad. Wing-pads small. Legs short, robust, almost smooth: order of length, 3, 2, 1. Claws not toothed underneath. Lateral caudal setae strongly fringed with hair on the inner margins, median seta fringed on both margins. The setae are rather less than half as long as the body, the median one being slightly shorter than the others. Latero-posterior angles of segments one to nine of abdomen are strongly toothed outwards in the shape of flanges with recurved backwardly-directed points. There is a median dorsal crest in the form of longitudinal carinations on the abdominal segments. Those of segments two to nine project backwards like the teeth of a saw, each over the segment posterior to it. Gills in the form of lamellate lobes, diversiform and marbled, their edges irregular, are borne on the first six abdominal segments: they are held lying over the dorsum and almost meet along the median line. There is also a very minute pair of gills attached to the posterior margin of the seventh segment.

There are three species, *O. wakefieldi*, McLachlan, described by Eaton (4) and found in the South Island many years ago, but since reported to be becoming extinct (2), *O. distans*, Eaton, noted by Hudson (1), and *O. intermedius*, a North Island species, the nymph of which has not been described, but which appears to be indistinguishable from *O. distans*.

Oniscigaster nymphs are by no means plentiful; they may be found in a number of places, generally in cold, moderately-flowing, well-bushed streams, very seldom in rivers, the banks of which have been cleared of bush, and this is probably because the birds destroy the winged stages if they have no shelter, for the large handsome sub-imago, emerging from its nymphal exuvia on a boulder, is a conspicuous object, and, moreover, it remains in this stage for three days before the final transformation. Consequently, its chances of achieving maturity are proportionately reduced.

The nymph is very sluggish, but its very inertness saves it from extinction by the trout, for these fish usually prefer moving food-organisms. Its marvellous camouflage makes it very difficult to find; furthermore, it often buries itself in the gravel.

Young specimens may be found in very fine gravel, but more mature nymphs occur in coarse gravel, boulders and rock pools. They prefer pools and slow currents, but not stagnant water.

The colour variation of this nymph is most remarkable: it is sometimes brown, sometimes greyish-green, sometimes whitish, sometimes reddish (a variety has red gills, but the usual colour is khaki); the legs and venter show two clearly-defined types, shown in the figures as type A and type B. Details of *O. intermedius* are illustrated (Pl. XVII, figs. 1 to 8).

Genus **Ameletus,** Eaton (1899).

Nymph torpedo-shaped. Head small. Antennae short. Eyes lateral. Labial and maxillary palps three-jointed. The canines coalesced. Wing-pads large and conspicuous. Legs, short, robust, sub-equal. Claws minutely toothed underneath. Abdomen tapering posteriorly. Latero-posterior angles of segments sharply toothed backwards. Caudal setae about half as long as body; the median seta is slightly shorter than the others and is plumose; the outer setae are thickly fringed with hair on the inner margins only. Simple lamellate gills are borne on the first seven abdominal segments; they are held laterally. The edge of the lamellae are finely toothed and the venation is pinnate.

It will be noticed that the mouth-parts in the species illustrated (Pl. XXII, figs. 5 to 9) are quite different from those of *Ameletus* spp. in the Northern Hemisphere, and when the adult characters of local species have been thoroughly re-examined, it is very likely that a new genus will have to be established for them.

There are two species, *A. ornatus* (Eaton) and *A. flavitinctus*, Tillyard. Hudson (1) has notes on the nymph of the former species, but that of the latter was only discovered in November 1929 in the river Wainui-o-mata, when a nymph, which I had captured there and which appeared to be a very dark variety of *A. ornatus*, transformed into a female sub-imago, which I was able to identify from Dr. Tillyard's paper (6) as *A. flavitinctus*.

Both nymphs will be described in another paper, but some of the details of the structure of *A. ornatus* are illustrated (Pl. XXII, figs. 1 to 9).

Ameletus nymphs are the best examples of the "swimmer" type of mayfly in New Zealand, their powers in this respect far exceeding those of any other Ephemerid species in this country.

Their distribution is widespread, and they occur in most streams except the very sluggish ones. They can exist either in swift currents or in the pools between rapids; they are found both on the upper and on the lower surfaces of boulders, as well as on their vertical sides; they are also found on vegetation at the edges of streams.

When at rest they have, more than any other mayfly nymphs, the curious habit of swaying their setae and the hinder part of the abdomen gently, at intervals, in a dorso-ventral arc.

The movement of these nymphs is so rapid that to the eye it appears as a swift wriggling dart, of which the component motions cannot be perceived. Careful and prolonged observation, however, shows that the movement is made by rapid dorso-ventral shakes of the "tail" and of the posterior part of the abdomen, through a short arc. The legs appear to be used to assist movement and are not held folded back against the body, as in the case of the American *A. velox*, Dodds (Dodds & Hisaw, 14).

Nymphs in captivity will often turn over on their backs, if disturbed, and appear as if dead; whether this is a simulation of death or an actual disturbance of balance due to unknown conditions is open to question; after an interval —which may vary from a few seconds to some minutes—they recover. When narcotised with chloral hydrate, they assume a similar posture.

The nymphs become full-grown during the summer months—though some do not transform till March, and a few even wait till April—when they leave the water and change to the sub-imaginal stage on a stone or boulder.

Genus **Ameletopsis,** gen. nov.

One other insect has been included hitherto among the New Zealand species of *Ameletus*, but for reasons given below (as regards the nymph) and elsewhere (as regards the winged stages), I have placed it in a new genus.

Description.

Structure adapted partly for swimming, partly for creeping. Body more or less flattened dorso-ventrally: head in much the same plane as body. Caudal setae short, sub-equal, fringed with hair on both sides; three in number. Gills on the first seven abdominal segments, consisting of large, round, entire, single, simple leaflets with central pinnate tracheae. Latero-posterior angles of abdominal segments prolonged backwards as sharp teeth. Eyes of male unlike female. Legs alike and sub-equal. Mouth-parts strongly developed; canines very long; palps multi-articulate.

Particulars of some of the structural features of this nymph are illustrated (Pl. XIX, figs. 1 to 8).

Ameletopsis perscitus, Eaton.

The nymph of this mayfly is unique in many respects. Its structure differs so markedly from that of the genus *Ameletus*, and moreover from that of the family or sub-family to which this genus is assigned by writers in the northern hemisphere, that there is little doubt that it has been incorrectly placed.

Indeed Tillyard (6) in his description of *Ameletus flavitinctus* states :—

> "It seems advisable here to point out that *A. perscitus*, Eaton, differs very greatly from both *A. ornatus*, Eaton, and *A. flavitinctus*, n. sp., in the shape of its wings, the density and regularity of their cross-venation and in the remarkable structure of its large-headed larva. These characters, taken together, suggest that it is not really congeneric with them. Further than this, a study of the three New Zealand species shows that they differ considerably from the genotype *A. subnotatus*, Eaton, from North America, and it appears probable that they may have to be placed in two new genera."

Hitherto, the larva does not appear to have been described, studied and compared with other larvae of the same genus, and the only notes on it are a few lines by Eaton (5), p. 291, and by Hudson (1).

Needham (8) considers the mayflies to be a single family and divides them into three sub-families, whereas Lestage (10) ranks them as an order and groups them in five families. However, Needham's sub-family BAETINAE corresponds very closely to Lestage's family BAETIDAE—*not* to be confused with his sub-family BAETINAE, for it is to his sub-family SIPHLURINAE that he assigns the genus *Ameletus*. Needham has no sub-division corresponding to this sub-family.

The species under discussion, *A. perscitus*, cannot be included in Lestage's genus *Ameletus* because the head of this species is not vertical but horizontal, the external edges of the gills are not toothed or haired but smooth, and their tracheal ramification is considerable, not "little ramified"; moreover the palps are not three-segmented but multi-articulate: this, also, takes it out of Eaton's nymphal group (p. 317 (4)), on which most of the work of Needham and Lestage is based, and puts it in a group with his unknown Chilian nymph, to which alone the mouth-parts of *A. perscitus* bear some resemblance, but the structure of other parts of these two is totally different. It cannot be included even in Lestage's sub-family SIPHLURINAE, to which he assigns the genus *Ameletus*, for this sub-family has the outer caudal setae fringed internally only, whereas those of *A. perscitus* are fringed on both sides.

Needham also groups various genera, among which is *Ameletus*, as having the outer caudal setae fringed only on the inner sides, and further states that in the genus *Ameletus*, the ends of the maxillae are fringed with pectinated hooks. *A. perscitus* does not correspond to this description.

Habits.

This nymph is carnivorous, feeding on small specimens of Leptophlebiid nymphs and other organisms.

Though found under stones in rapid water, its favourite haunt is some dark, still backwater or a shallow, slowly-flowing portion at the edge of a stream. Here it will lie perfectly still on a stone or in a crevice, except for an occasional movement of the gills, its camouflage colouring making it very difficult to detect. At times, it will walk forward with a gliding motion for a few inches, "freeze" for some seconds, and then move forward again. It has a habit of brushing its mouth-parts with its anterior pair of legs. Another characteristic is its trick of peering cautiously round the edge of a stone and stalking slowly forward. Though sluggish, when thoroughly disturbed it can move with considerable rapidity, swimming strongly with quick, somewhat jerky movements of its body.

It becomes full-grown from December to March, when it crawls on to a stone above water-level to transform to the sub-imaginal stage.

This species occurs throughout the Wellington, Hawkes Bay, Nelson and Canterbury provincial districts, and is moderately abundant and evenly distributed.

The adult has been described by Eaton (5). Examination of the imago shows certain differences between it and the general type of *Ameletus*, which are sufficient, when taken in conjunction with those of the nymph, to justify making a new genus for it.

Family LEPTOPHLEBIIDAE.

This family, which contains mainly the smaller mayflies, comprises more than half the species in New Zealand. Some of them are very much alike and hard to distinguish from each other, and it will probably be a considerable time before all the species in this country have been identified and described.

Five species of LEPTOPHLEBIIDAE were known until recently; during the last three years, I have found eight new ones, making a total of thirteen species. They form a heterogeneous group, the species being much alike, in sharp contradistinction to the species of the SIPHLONURIDAE, which are extraordinarily diversiform.

Needham (8) has no equivalent division, for although his sub-family BAETINAE would cover all the genera in our family LEPTOPHLEBIIDAE, it would also embrace most of the SIPHLONURIDAE as well.

Lestage (10) has a sub-family LEPTOPHLEBIINAE of his family BAETIDAE, which would fit, with one modification. He states :—". . . Sept paires de branchies tantôt semblables et, dans ce cas, toutes filamenteuses, tantôt dissemblables et alors la première paire rudimentaire et les six suivantes plus ou loins lamelliformes. . . ."

In the case of New Zealand species, the gills of the first pair (of the latter alternative) are not rudimentary and are kidney-shaped.

Description.

Nymph of the crawling type: body more or less flattened dorso-ventrally. Eyes lateral. Antennae long and filiform. Mandibles short, not extending in front of head. Maxillary and labial palps three-segmented. Galea-lacinia of maxilla terminating apically in a broad brush of brown hair and a number of minute pectinate rakes. Wing-pads generally prominent. Legs long, spinose: femora oval: claws toothed underneath. Posterior-lateral angles of segments of posterior half of abdomen toothed backwards. Caudal setae long, median ones usually slightly the longest: whorled on both sides with very short hairs. Gills borne laterally on the first seven abdominal segments, sometimes alike and then in the form of a bifid lash, sometimes dissimilar and then the gills of the first pair are kidney-shaped, those of the remaining pairs round or ovate.

There are two genera, the one, *Atalophlebia*, with double gills, the other, *Deleatidium*, with single ones.

Genus **Atalophlebia,** Eaton (1881).

Nymph of the crawling type. Body somewhat flattened dorso-ventrally. Eyes lateral. Antennae long and filiform. Maxillary and labial palps three-segmented. Labrum always less than three times as broad as it is long and notched medio-anteriorly. Maxilla with broad terminal brush of long brown hairs and small pectinate rakes. Wing-pads large. Legs, long, spinose: femora usually somewhat dilated: claws toothed underneath. Latero-posterior angles of abdominal segments mostly toothed backwards, pronouncedly so in the posterior half. Caudal setae of varying length, minutely haired at segmental junctions; median one longest. Pairs of gills borne laterally on the first seven abdominal segments: the gills are double and consist of a double lash or pair of lanceolate or ovate-acuminate lamellae: venation pinnate. The gills of the posterior pair are often aborted.

It should be noted that the nymphal characters of our species differ somewhat from those defined as generic characters by Needham and Murphy (9).

For example :—" Posterior-lateral angles of rear abdominal segments not tipped with thin flat lateral spines. . . ." On the contrary, our nymphs have teeth or spines in these segments, notably *A. cruentata.* Again, ". . . Femora regularly tapering from near the base, not dilated. . . ." In our species, the femora *are* dilated and the broadest part is at or near the middle of this segment. Further, the labrum could hardly be described as " narrowly elliptical " and the " acute median notch in front " is sometimes merely a slight curved identation.

On p. 36 *tom. cit.*, however, there is a conflicting description of Atalophlebiid nymphal characters, and the nymphs are described as having lateral spines on abdominal segments 5 to 9 and the femora as dilated.

The other characters specified on this page do not agree with the characters of our species, *i.e.* the distal tooth under the tarsal claw is not minute—compared with the others—but slightly larger, the width of the labrum does not exceed the length three times but is not quite twice as long, and the glossae are not conic-pointed in any of our species.

Some structural features of a typical species, *Atalophlebia versicolor*, are illustrated (Pl. XVIII, figs. 1 to 10).

All the members of this genus are found either among debris in the river bed in slow-flowing parts of streams, e.g. *A. versicolor*, or among stones or shingle in slow (*A. cruentata*) or moderately-flowing parts of streams (*A. nodularis*). They are poor swimmers, moving with a jerky, awkward, undulating motion of the body, agitating the legs rapidly and closing the setae, which are normally held well spread out. They can, however, edge sideways and retreat backwards with great agility, and when pursued do so, seeking shelter in a crevice or under a stone and seldom attempting to escape by swimming away. To try and capture a number of nymphs of this genus (especially *A. cruentata*) is to receive an object lesson in minor tactics and the use of ground and cover.

The nymphs of *A. versicolor* and *A. dentata* are much alike, the latter is figured by Hudson (1) and the former may be distinguished from it by the yellow longitudinal stripe, which it bears, placed medianly, on the dorsum.

A. cruentata is bright orange-red and therefore easily recognisable. *A. nodularis* is like a small edition of *A. cruentata*, but is dull-coloured. Lillie (3) figures it, but his drawing is not much like the nymph and the description is very meagre. Its gills, unlike those of the other species, which are all of the *A. versicolor* type (Pl. XVI, fig. 8), are each composed of a bifid lash, each component of which has a strong, central, unbranched trachea.

Genus **Deleatidium**, Eaton (1899).

Nymph of the crawling type. Body markedly flattened dorso-ventrally. Nymphs generally found under stones. Head square. Eyes lateral. Antennae long and filiform. Maxillary and labial palps three-segmented. Labrum at least three times as broad as it is long and notched medio-anteriorly. Maxilla with broad terminal brush of long brown hairs and small pectinate rakes. Wing-pads large. Legs long, spinose; femora very much dilated; claws toothed underneath. Latero-posterior angles of abdominal segments mostly toothed backwards, pronouncedly so in the posterior half. Caudal setae as long as or longer than the body; median seta longest. Pairs of gills borne laterally on the first seven abdominal segments : the gills are single : those of the first pair are kidney-shaped those of the other pairs are ovate-acuminate or sub-rotund.

There are slight differences in the characters of *Deleatidium* nymphs referred to here and those ascribed to that genus—with reference to neotropical species —by Needham and Murphy (9).

This genus was established by Eaton from preserved specimens of a single species sent to him from New Zealand; he distinguished it from *Atalophlebia*, in that in the latter genus the nymphs had double gills and the adults had claws alike in each tarsus, whereas in *Deleatidium* the nymphs had single gills and the adults had claws dissimilar in each tarsus.

The discovery of several new species during my researches has shown that the classification of the LEPTOPHLEBIIDAE is by no means as simple as it appeared at first. Discussion of this matter will be left to another paper as adult characters are involved, and, for present purposes, *Deleatidium* nymphs will be considered as Leptophlebiids with single gills.

With the exception of the gills, there are no differences of major importance between the nymphs of *Deleatidium* and those of *Atalophlebia*. In the former genus the body is rather more pronouncedly flattened dorso-ventrally, the labrum is perhaps longer and narrower and always has a decided median notch in the anterior border, the femora are always dilated and are flattened dorso-ventrally, the head is square (in *Atalophlebia* spp. it is more rounded anteriorly), and the caudal setae are never shorter than the body, as they sometimes are in *Atalophlebia.*

Deleatidium nymphs are found mainly on the under surfaces of stones in waters of varying rapidity. They are difficult to dislodge; in fact, *D. myzobranchia*—a species with rounded gills—appears to use its gills sometimes as suckers. Species of this genus are also found buried in the sand and shingle of the river-bed and—especially in winter—among submerged moss and waterside vegetation.

Three of the species, *D. lillii*, *D. vernale* and *D. autumnale*, are so much alike that they can only be differentiated, with certainty, when they transform.

Individuals of *Deleatidium* spp. are more numerous than those of any other genus, perhaps because of their superior adaptability to different conditions, such as the rate of flow of the current and the variation in oxygen content of the water.

In the Wellington district, nymphs of *D. lillii* have been seen to metamorphose almost all the year round, even in midwinter.

It is of interest to note, however, that two specimens (one male and one female), which were secured as nymphs on July 4th, 1929, changing the same day into sub-imagines, failed to reach the imaginal stages. They attempted to do so in the laboratory about thirty-six hours later, but apparently had not the necessary energy and died, partly metamorphosed. Whether this is usually, or perhaps often the case in winter is not known.*

Deleatidium nymphs are extensively eaten by trout and by other fish, as well as by predatory insects such as the nymphs of some stoneflies and the larvae of carnivorous aquatic beetles; they have other enemies, also, for Nematode worms may often be found in their stomachs.

ACKNOWLEDGEMENTS.

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* In further transformations during June 1930, this experience was repeated.

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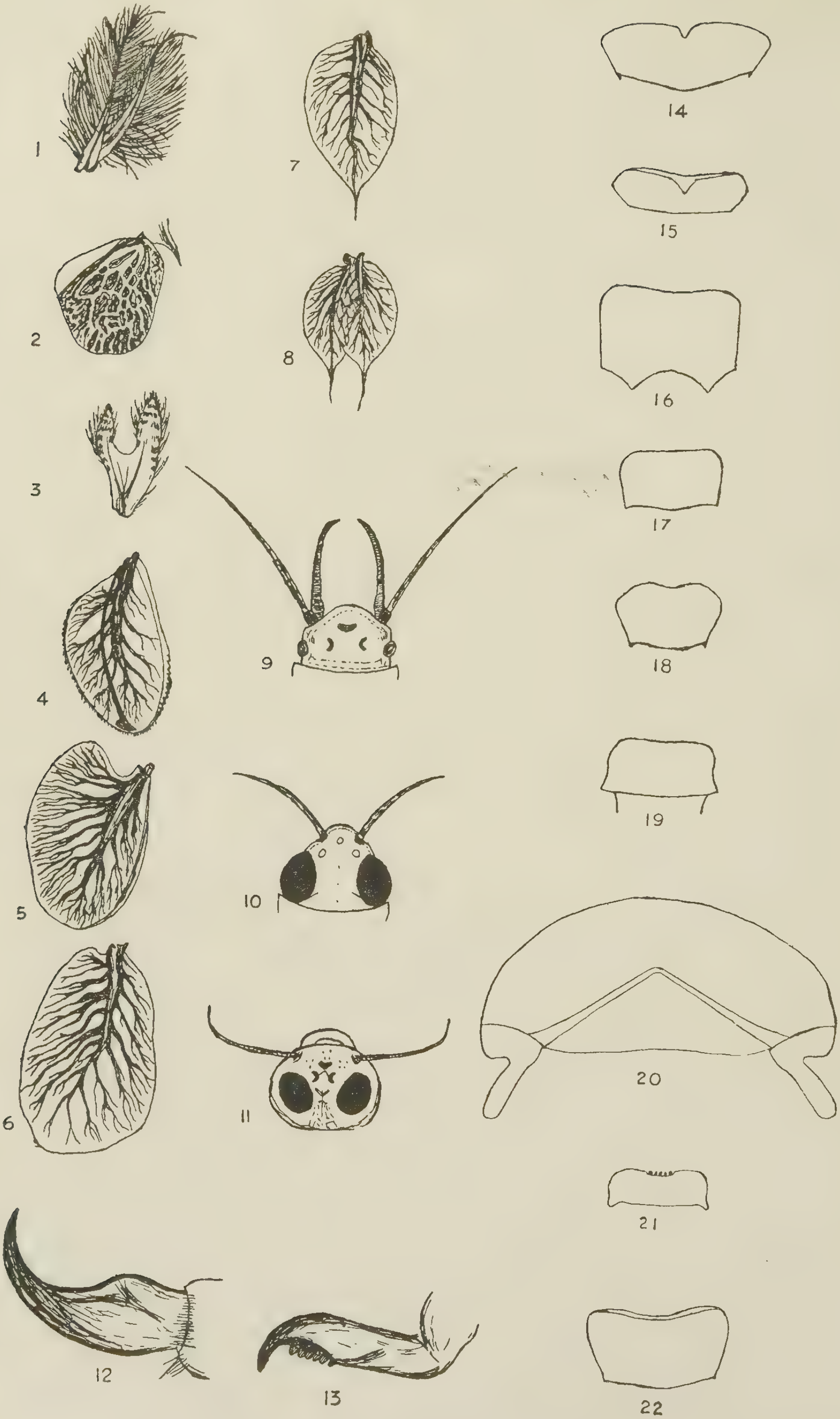
Plate XVI.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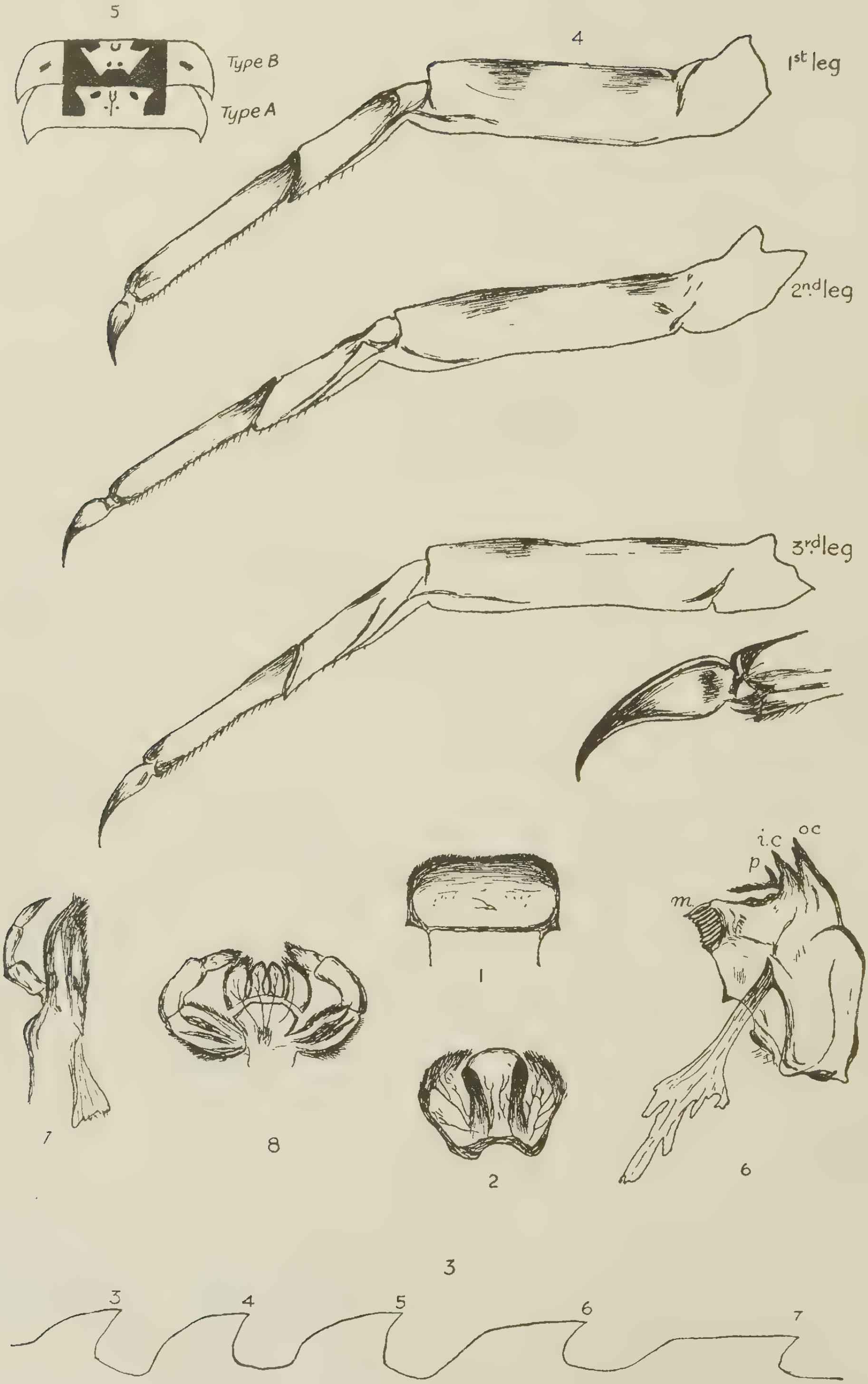
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EXPLANATION OF PLATES XVI–XXII.

PLATE XVI.

Gills.

FIG. 1. *Ichthybotus hudsoni.*
2. *Oniscigaster intermedius.*
3. *Coloburiscus humeralis.*
4. *Ameletus ornatus.*
5. *Ameletopsis perscitus.*
6. *Deleatidium myzobranchia.*
7. *Deleatidium vernale.*
8. *Atalophlebia versicolor.*

Heads.

9. *Ichthybotus hudsoni.*
10. *Ameletus ornatus.*
11. *Ameletopsis perscitus.*

Claws.

12. Family SIPHLONURIDAE.
13. Family LEPTOPHLEBIIDAE.

Labrum of Nymphs.

14. *Deleatidium vernale.*
15. *Deleatidium myzobranchia.*
16. *Ameletus ornatus.*
17. *Coloburiscus humeralis.*
18. *Ichthybotus hudsoni.*
19. *Oniscigaster intermedius.*
20. *Ameletopsis perscitus.*
21. *Atalophlebia cruentata.*
22. *Atalophlebia versicolor.*

Note.—The different figures are not drawn to the same scale.

PLATE XVII.

Oniscigaster intermedius (Eaton).

FIG. 1. Labrum, × about 20.
2. Hypopharynx, × about 20.
3. Dorsal crest (3rd to 7th segments), × about 14.
4. Legs, × about 14; claw, × about 30.
5. Types of ventral abdominal segment (diagrammatic).
6. Left mandible, × about 20.
7. Right maxilla, × about 20.
8. Labium, × about 20.

PLATE XVIII.

Family LEPTOPHLEBIIDAE.

FIG. 1. *Atalophlebia versicolor :* thorax and abdomen (dorsal view), × 12½.
2. do. do. legs, × 12½.
3. do. do. tarsal claw, × 60.
4. do. do. right maxilla, × 12½.
5. do. do. left mandible, × 12½.
6. do. do. labrum, × 12½.
7. do. do. labium, × 12½.
8. do. do. gills, *ca.* × 12½.
9. do. do. superlinguae, *ca.* × 25.
10. do. do. maxillary rake, much enlarged.
11. do. do. anterior gill, *ca.* × 12½.
12. *Deleatidium vernale*, gills, *ca.* × 7½.

PLATE XIX.

Ameletopsis perscitus (Eaton).

FIG. 1. Nymph. Head.
2. do. Labrum, × about 11.
3. do. Left mandible, × about 11.
4. do. Labium and Hypopharynx, × about 11.
5. do. Left maxilla, × about 11.
6. do. Dorsum of 6th abdominal segment.
7. do. Legs.
8. do. Gills.

PLATE XX.

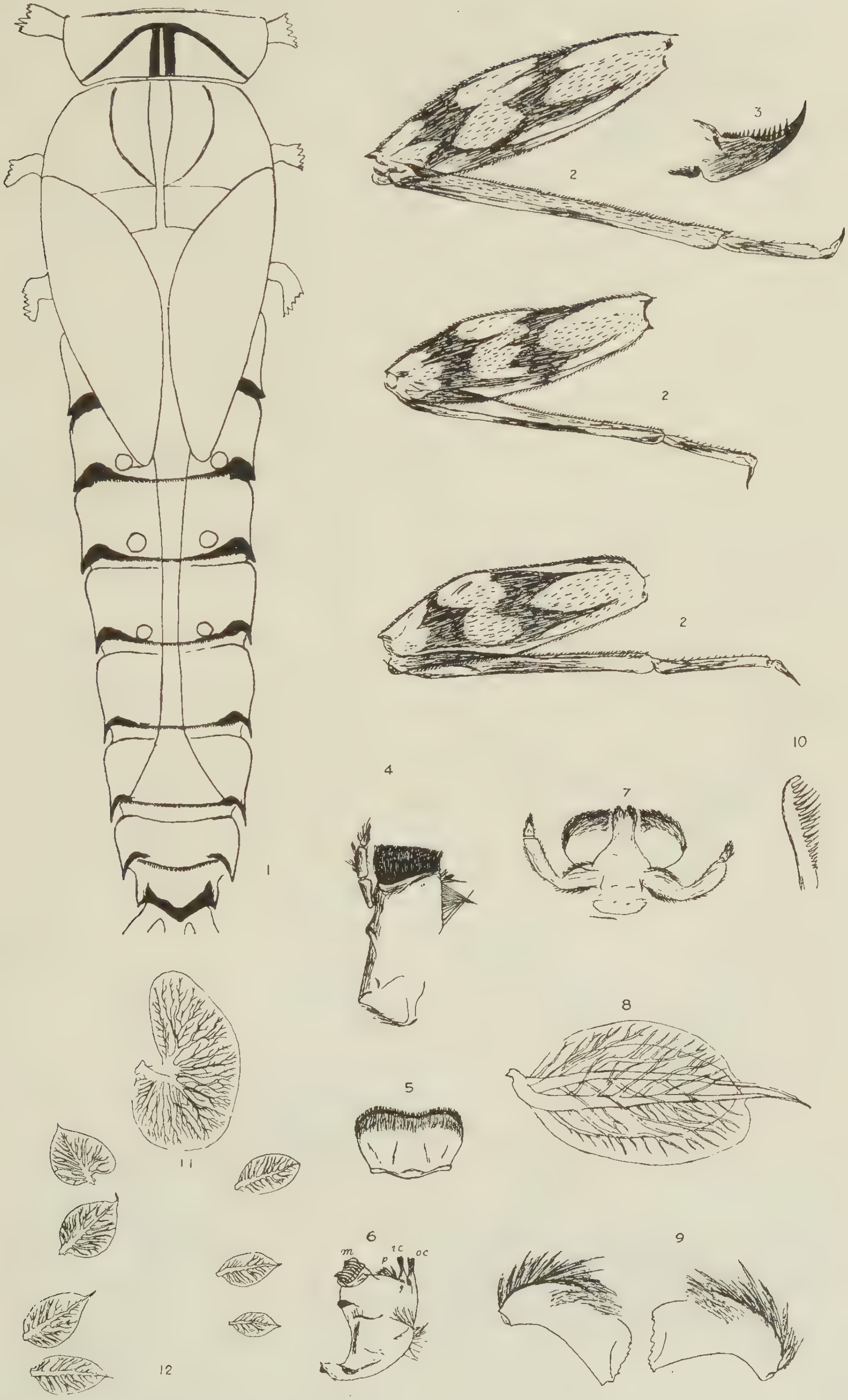
Ichthybotus hudsoni.

FIG. 1. Hypopharynx, × about 30.
2. First pair of gills.
3. Second pair of gills, × about 12.
4. Head (dorsal view), × about 12.
5. Labium, × about 30.
6. Mandible, × about 30.
7. Maxilla, × about 30.
8. Labrum, × about 30.
9. Feathered hair from leg, much enlarged.
10. Claw of third leg, much enlarged.
11. Legs, × about 12.

PLATE XXI.

Coloburiscus humeralis (Walker).

FIG. 1. Immature nymph, × about 12.
(In order to show the lateral edges of abdominal segments, the gills on the left are omitted.)
2. Legs, × about 12; tarsal claw, much enlarged.
3. Maxilla, *ca.* × about 25.
4. Labrum, × about 25.
5. Gill, × about 12.
6. Labium, *ca.* × about 25.
7. Mandible, *ca.* × about 25.
8. Canine region of mandible, enlarged.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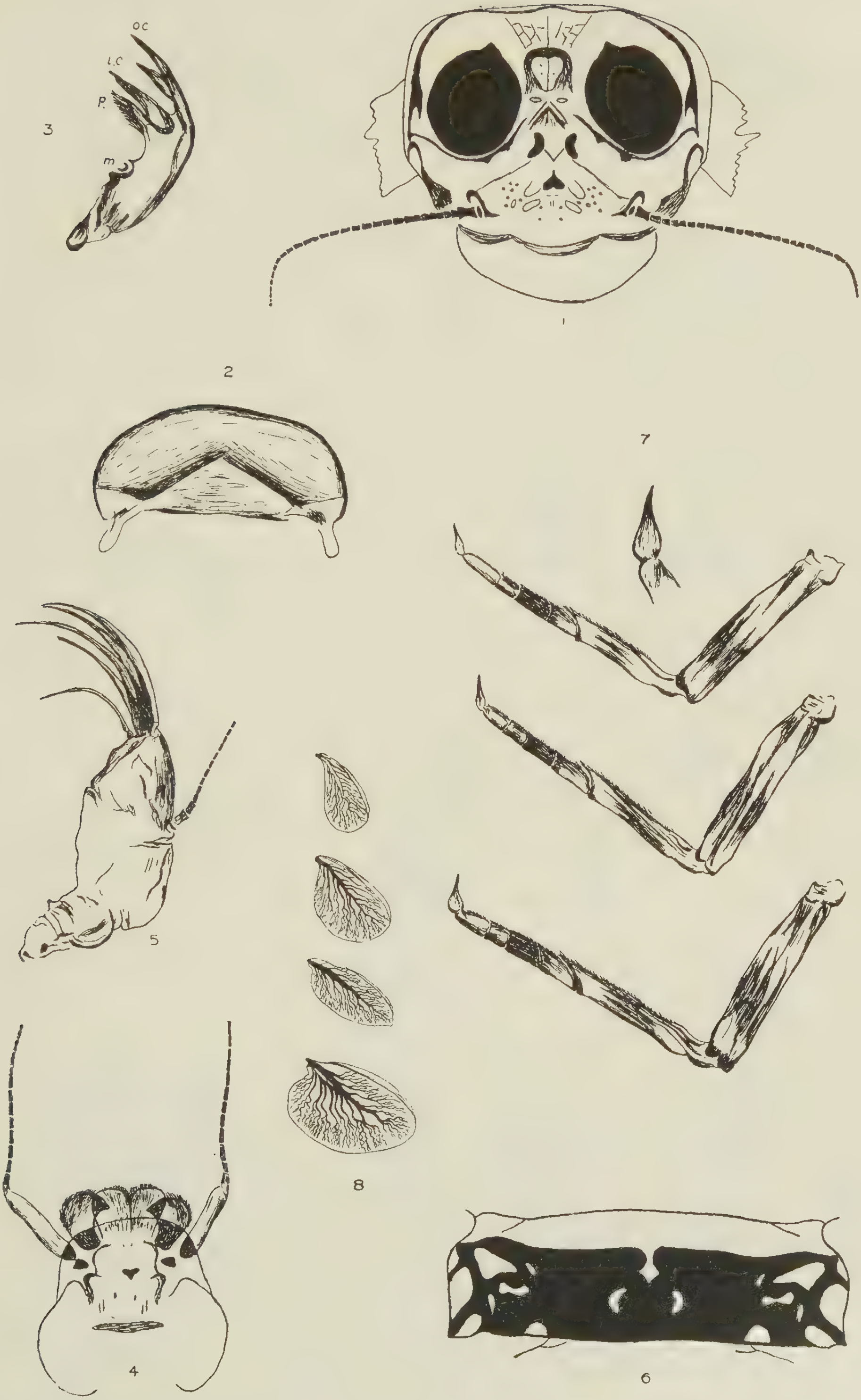
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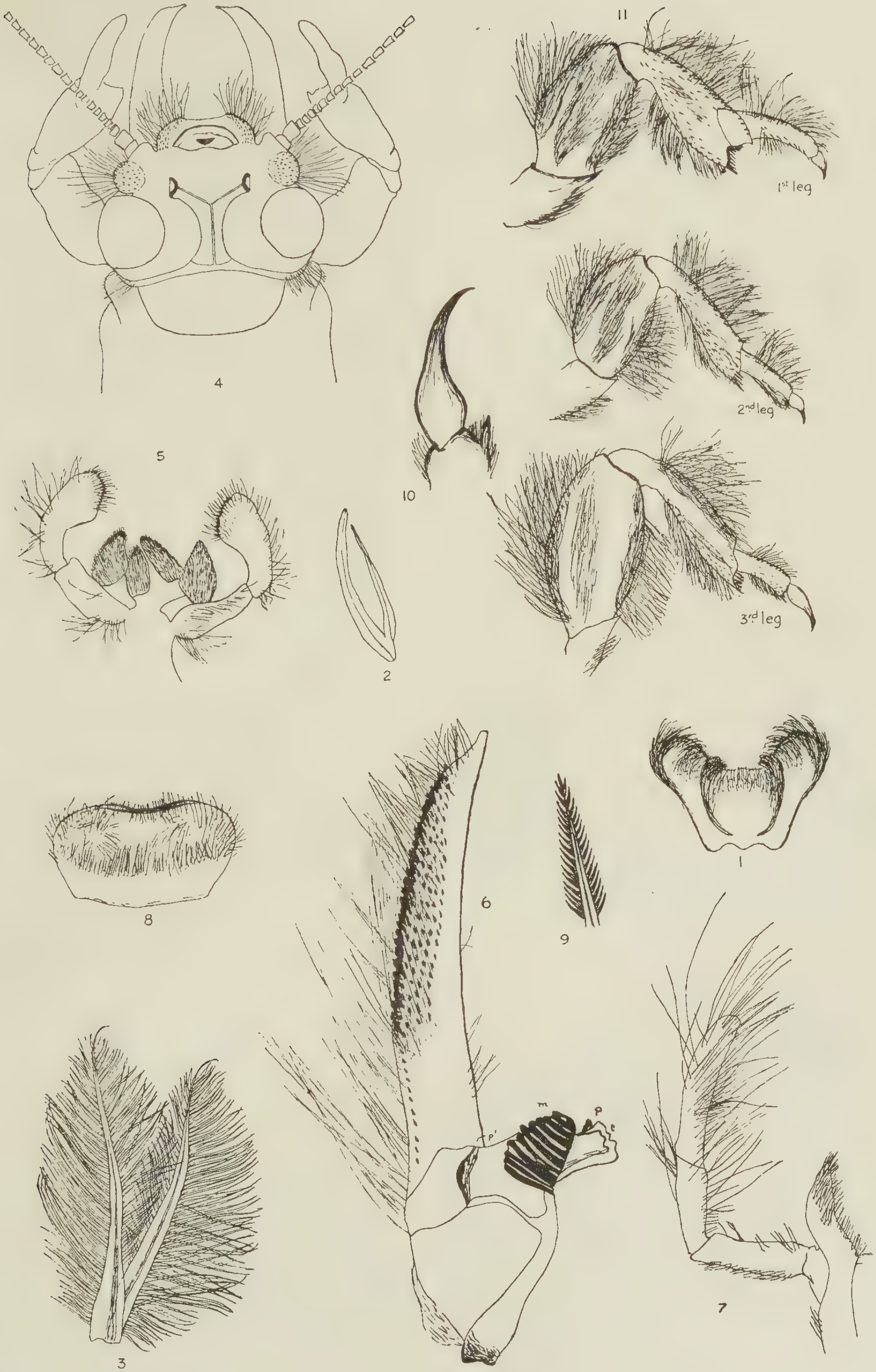
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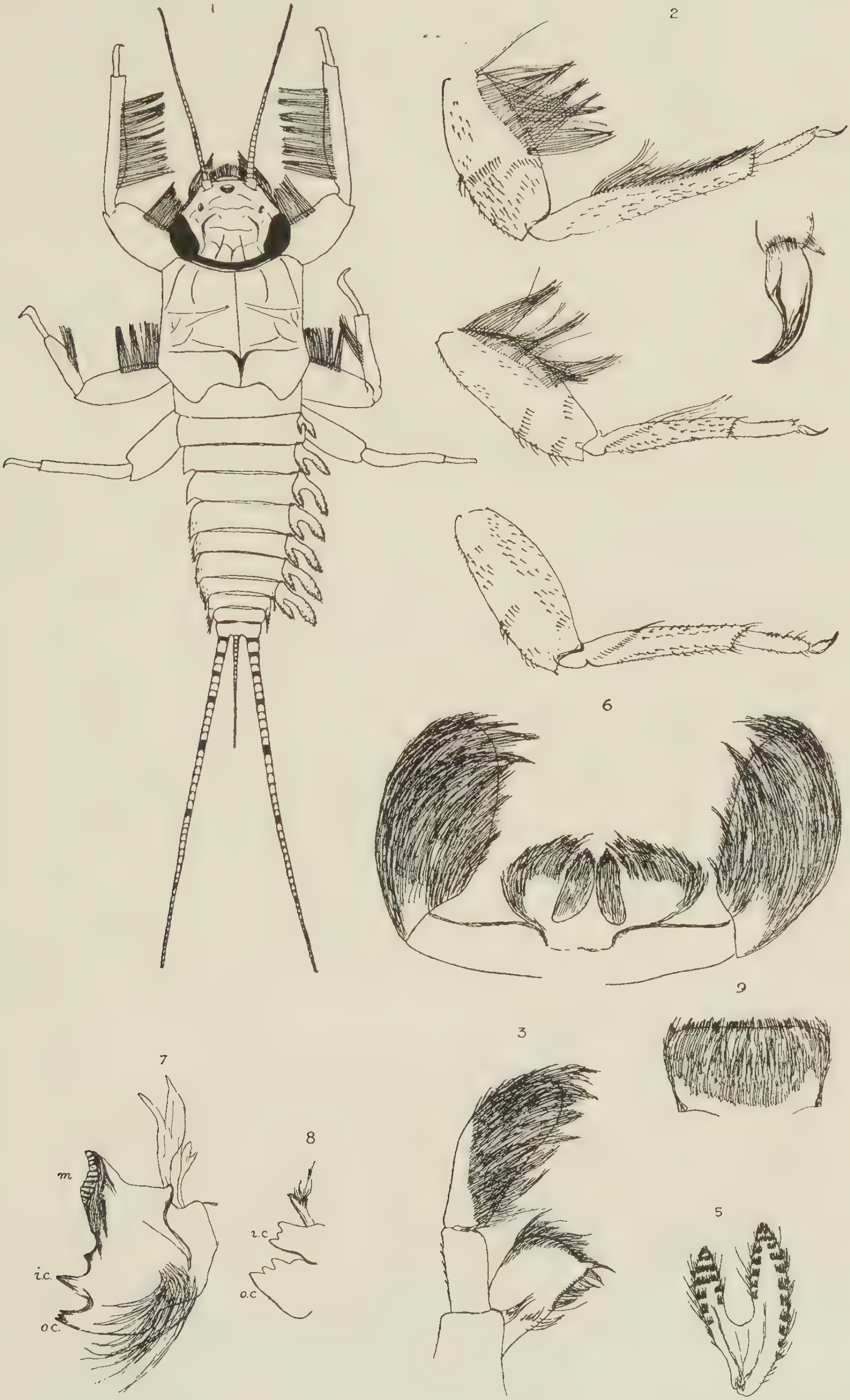
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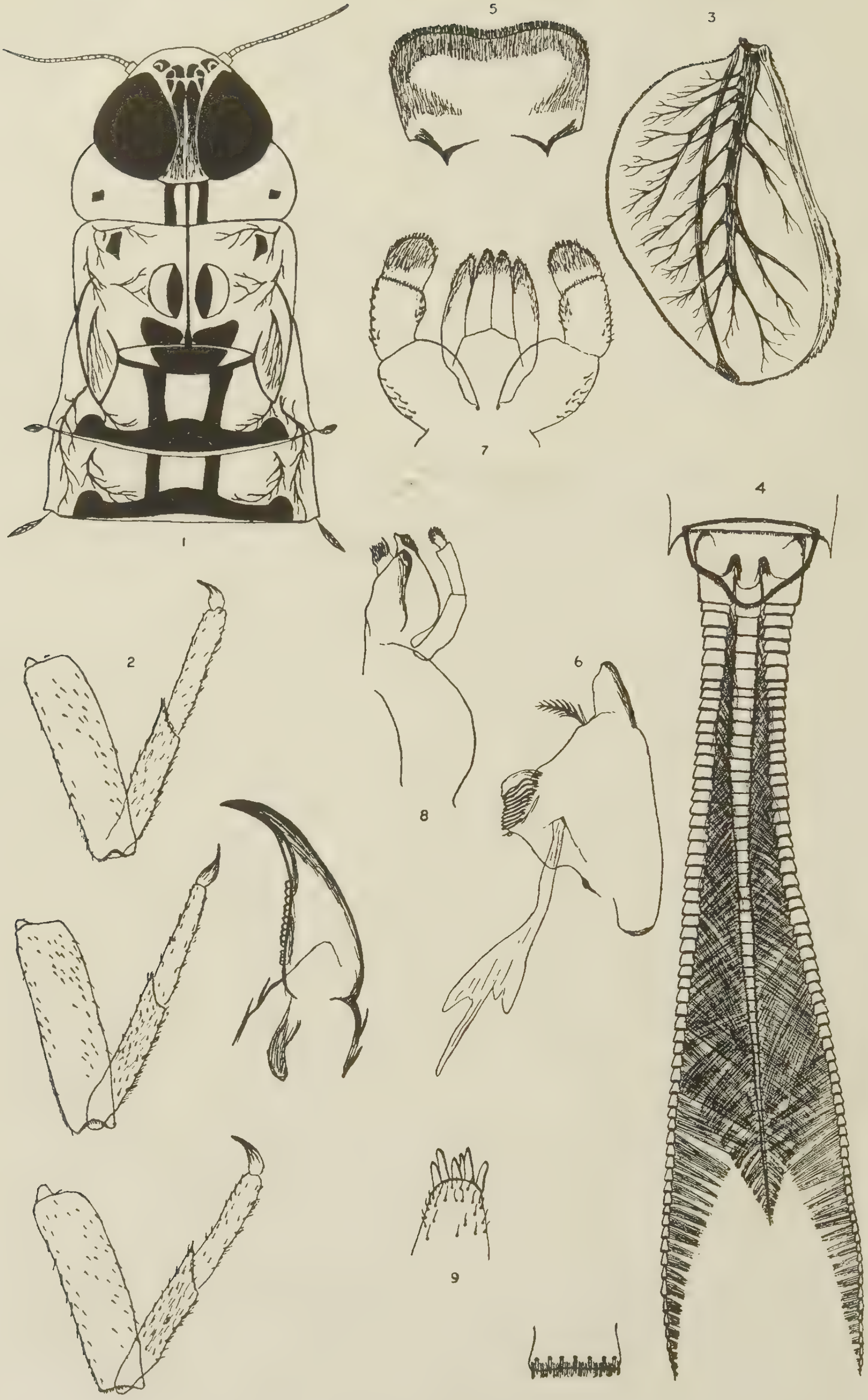

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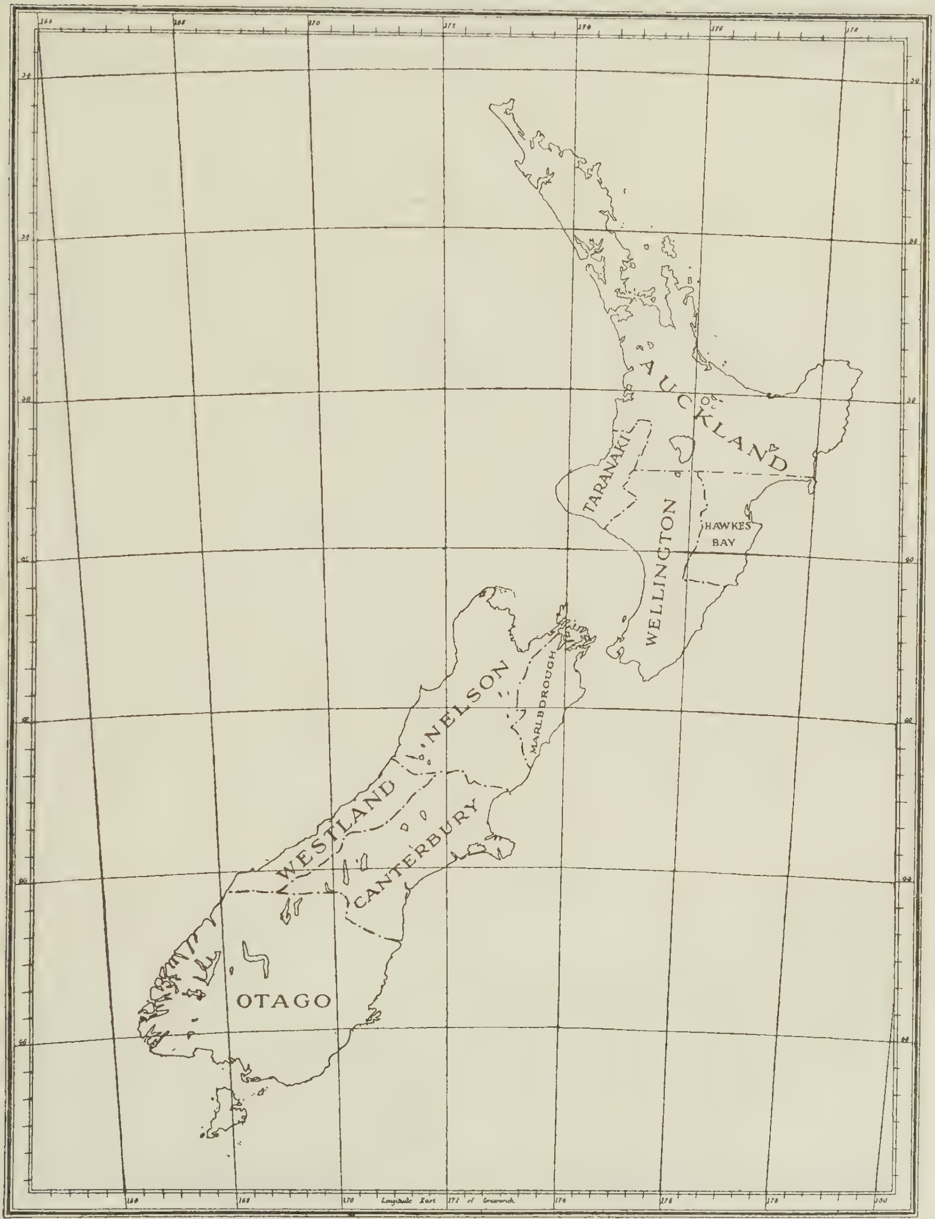
Plate XXII.

Ameletus ornatus (Eaton).

Fig. 1. Thorax and first two abdominal segments, × about 14.
(Immature nymph; wing-pads undeveloped.)
2. Legs, × about 14; tarsal claw, much enlarged.
3. Gill, × about 14.
4. Caudal setae, × about 14, and segment of one, much enlarged.
5. Labrum, × about 25.
6. Mandible, × about 25.
7. Labium, × about 25.
8. Maxilla, × about 25.
9. Tip of glossa, much enlarged.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Map of New Zealand.

THE EARLY STAGES OF TWO SPECIES OF RHIPICERIDAE (SANDALIDAE) FROM INDIA

By J. C. M. Gardner, I.F.S.
(Forest Research Institute, Dehra Dun, U.P., India.)

[Read 4th March, 1931.]

Plate XXIV.

The few known larvae of the family Sandalidae (until recently known as Rhipiceridae) fall into two categories: first the very hard-skinned, cylindrical, rotten-wood-boring type (*Callirrhipis*); and second the soft, fusiform, parasitic type represented by *Sandalus*; the only known larva of the latter genus has been described by Craighead,* who points out that although the form and many structures are greatly modified, fundamental characters are not greatly affected by the peculiar habit. He considers, however, that the larva of *Sandalus* has sufficient peculiarities to warrant the formation of a separate family to include the genus. An interesting parallel is found in the case of the larva of *Hectarthrum trigeminum*, Newm. (Cucujidae), described by Gravely †; a larva of the same genus, probably *H. heros*, F., is found in Dehra Dun in the pupal cells of *Aeolesthes holosericea*, F. (Cerambycidae), and of *Belionota prasina*, Thunb. (Buprestidae); the larva of *Hectarthrum* is superficially quite unlike the active larvae of other Cucujidae, although possessing the essential larval characters of that family; the larva of *Hectarthrum* and that of *Sandalus*, although fundamentally quite distinct, have a similar body form and analogous structural modifications, an instance of convergence due to parasitic habits. The early larval instars of these genera are not known, but they probably resemble the more active larvae of related genera.

Callirrhipis and **Parennometes.**

The larvae of the two species, one from each genus, described below, have the following common characters. Body cylindrical, and, except for connecting membranes, very hard and corneous. Setae very sparse. Head subglobular, partly retractile into thorax; epicranial suture well developed; gula well developed. Ocelli not evident. Antennae retractile, small, with two well-developed corneous basal joints and a minute unisetiferous apical papilla which may perhaps represent a third joint. Labrum rigidly corneous, transverse, with sinuate margin. Clypeus membranous. Ventral mouth-parts retracted, forming a compact unit to which a basal membranous fold allows movement. Maxillary stipes very wide, extending to the median line posteriorly; maxillary palp three-jointed, borne on a basal joint-like palpiger; cardo transverse; mala (fig. 4, *ma*) short, bluntly rounded at apex, and with an obtuse protrusion from the inner margin which possibly represents a rudimentary lacinia. Labium with rigidly corneous, transverse ligula; palps two-jointed; the mental region

* 1921, *Proc. Ent. Soc. Wash.*, **23**: 44–48; pl. 4.
† 1916, *Rec. Ind. Mus.*, **12**: 150–151, pl. 22, figs. 18–22.

consists of an anteriorly wide, posteriorly attenuate, plate which separates the maxillary stipites for only the anterior two-thirds or so of their length. Prothorax distinctly longer dorsally than ventrally, with a shallow, more or less vertical, groove on each side behind the apex. Typical abdominal segments with tergite, pleurites and sternite fused to form a cylinder, the lines of fusion not evident. Abdominal segment 8 with an oblique striate groove on each side. Segment 9 forming a sub-vertical operculum; posterior end of the body with a truncate appearance. Spiracles biforous. Legs small, corneous, the coxae of each pair nearly contiguous medially.

Generic Characters.

The larvae of the two species under discussion are separable by very distinct characters of generic importance.

Parennometes: First two thoracic segments asperate above. Striate impressions present only on abdominal segment 8. Deep foveae are present only on the 7th abdominal segment. Segments 7 and 8 each with a pair of small spines dorsally. The operculate 9th segment concave, finely granulate. Legs with the four distal joints apparently fused together, claw not distinct. (*P. gardneri*, van Emden.)

Callirrhipis: Thoracic segments not asperate above. Striate impressions present on each side of the ten segments behind the prothorax. Abdominal segment 2 to 7 each with a pair of very deep foveae. Abdominal segments 7 and 8 without spines. Caudal operculum convex. Legs with five distinct joints, the distal one a claw. (*C. nigrescens*, van Emden.)

Parennometes gardneri, van Emden.*

Larvae, pupae and beetles were taken from a rotten log, S. Mangalore, Madras, May 1930 (J. C. M. G.).

Larva.

(Pl. XXIV, figs. 1, 2, 4 to 8.)

Castaneous, black towards extremities. Slightly expanded posteriorly. Length about 35 mm.

Head rather coarsely and closely punctate, each puncture with a seta; most of the setae extremely short, a few long. Frons without distinct depressions. Epicranial suture nearly as long as frons. Gula about as long as maxillary stipes.

Antennae (Pl. XXIV, fig. 8) with basal joint cylindrical, longer than wide; second joint rather stout, longer than wide and with a softer zone near the blunt apex; a continuation from the more corneous skin passes through this softer zone and bears on its apex a minute unisetiferous papilla.

Labrum (Pl. XXIV, fig. 6) nearly black, rigid, with rounded lateral lobes and a pair of rounded median convexities of the anterior margin. Mandibles (Pl. XXIV, fig. 5) with three blunt apical teeth and behind those, two marked marginal convexities, one on dorsal, one on ventral, edge.

Maxillae with mala as shown on Pl. XXIV, fig. 4. The palpiger and two basal joints of palp transverse, the distal joint slightly longer than wide, tapering slightly at the apex. Labium (Pl. XXIV, fig. 4) with two-jointed palps, each joint slightly longer than wide, the basal one stouter.

Pronotum and mesonotum with numerous short, transversely carinate asperities

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* 1931, *Ent. Blätter*, **27**: 58.

(Pl. XXIV, fig. 1). The following seven segments smooth, with very fine, sparse punctures; certain segments have faint and short impressed lines near the anterior margin, but there are no striate depressions (except on 8th segment) or deep foveae (except on 7th segment). The 7th abdominal segment (Pl. XXIV, figs. 1, 2) near the middle with a subdorsal pair of deep foveae, connected by a shallow transverse groove, and, between them a pair of small posteriorly directed spines. The 8th segment with a distinct oblique striate groove on each side and, on the posterior dorsal margin, a pair of small, posteriorly directed spines; this margin is finely irregular on each side of the spines.

The terminal operculum is distinctly concave, granulate and with several minute setae; a transverse suture near the dorsal margin of the operculum may indicate the line of fusion of the 8th and 9th segments. These two segments are somewhat enlarged ventrally. The anal segment is normally concealed.

Spiracles biforous. Legs (Pl. XXIV, fig. 7) short and stumpy, each consisting of a distinct basal joint or coxa and a second part apparently consisting of the fused distal joints; there is no distinct claw, although it is possibly represented by the largest of several apical teeth or tubercles.

Pupa.

(Pl. XXIV, fig. 3.)

Abdomen elongate, slender. Wings extending about to apex of 2nd abdominal segment. Antennae, prothorax, etc., very much as in imago. Frons with numerous setiferous asperities. Pronotum finely asperate. The first eight abdominal tergites rather closely covered with biramous, acute asperities (Pl. XXIV, fig. 3). The seventh tergite with a post-median pair of circular glabrous depressions.

Callirrhipis nigrescens, van Emden.*

Two beetles, a larva, and fragments of exuviae were taken from a rotten log, S. Mangalore, Madras, May 1930 (J. C. M. G.).

Larva.

(Pl. XXIV, figs. 9 to 13.)

Reddish castaneous, blackish towards extremities. Length about 30 mm.

Head with fairly close fine punctures. Frons with a very shallow transverse discal depression. Labrum as shown in Pl. XXIV, fig. 13.

Mandibles (Pl. XXIV, fig. 12) apically tridentate, and near the middle, with two minute teeth on ventral cutting margin and one on the dorsal margin.

The striate impressions on each side of the last two thoracic segments slightly sinuate, long; those on the first abdominal segment each subdivided into two parts; those on abdominal segments 2 to 7 rather small, separated by about their own length, or a little more, from the deep foveae above them. The foveae with thickened margin and the cavity with numerous setae. The caudal operculum apparently formed by the 9th tergite, convex, finely punctate and with some extremely short setae; the dorsal margin of the operculum even. The 9th sternite (Pl. XXIV, fig. 10, *st* 9) small, normally concealed. Legs (Pl. XXIV, fig. 11) short and stout, with five distinct joints, the last a claw.

In this larva the two anterior pairs of lateral impressions are not continuously striate, as each has a smooth zone near the middle, but it is possible that this is an individual variation. In a separate series of larvae from the same locality, but not associated with adults, these impressions are continuously striate.

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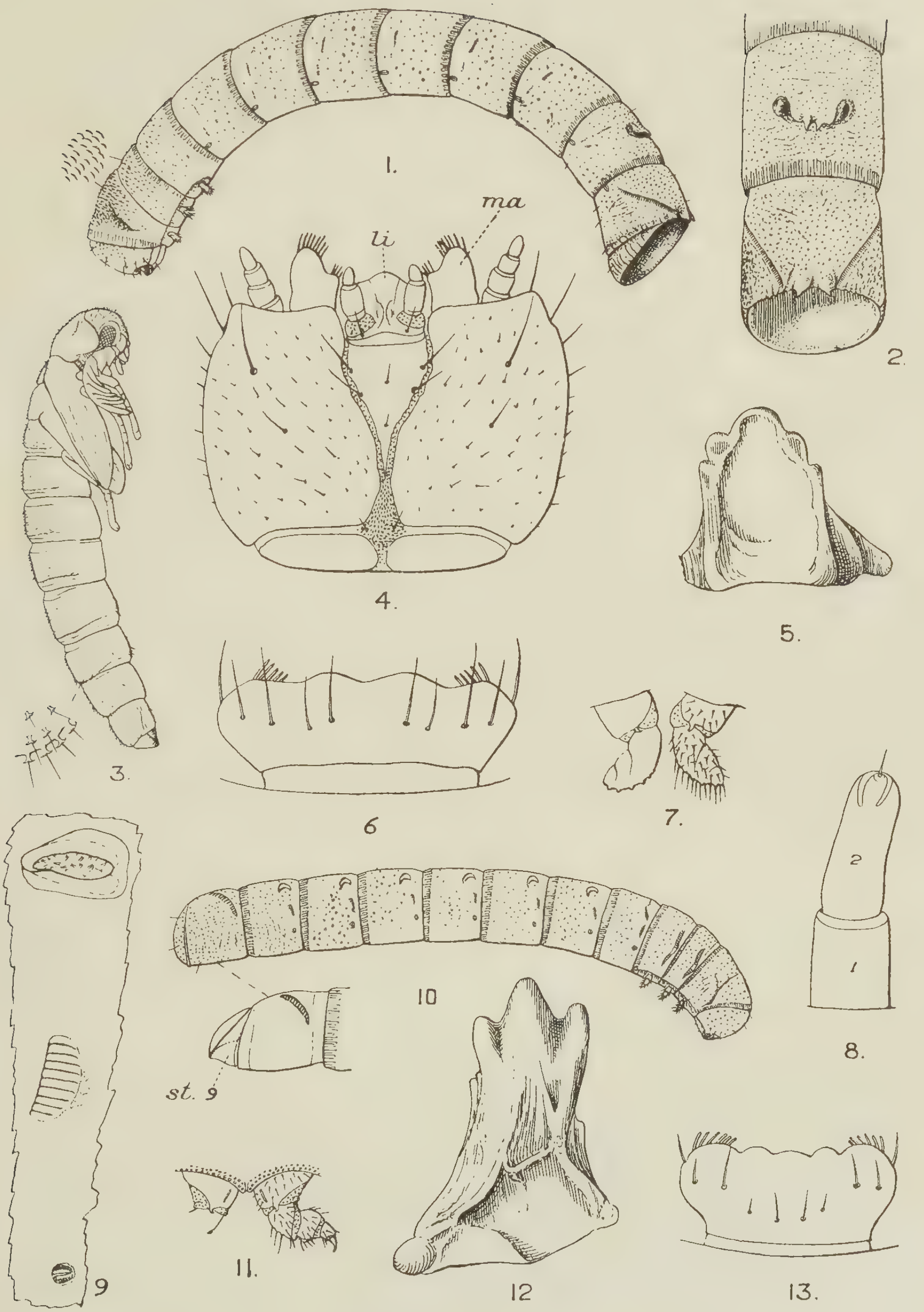
* *l.c.*, 56.

The larva of *C. dejeani*, Latr., as figured by Schiodte (I have not seen the text of his description) appears to have, first, a pair of very distinct foveae on the frons (represented by a shallow groove in *nigrescens*), and second the operculum with a crenulate dorsal margin.

In conclusion I should like to express my thanks to Dr. Fritz van Emden for dealing with the adults of these two species and for returning the types for deposit in the British Museum.

EXPLANATION OF PLATE XXIV.

FIG. 1, 2, 4–8. Larva of *Parennometes gardneri*, van Emden.
  (1) Lateral view.
  (2) Dorsal view of caudal segments.
  (4) Ventral mouth-parts : *li*, ligula ; *ma*, mala.
  (5) Left mandible, ental view.
  (6) Labrum.
  (7) Prothoracic legs.
  (8) Antenna.
3. Pupa of *Parennometes gardneri*, van Emden ; some of the bifurcate spines shown enlarged.
9–13. Larva of *Callirrhipis nigrescens*, van Emden.
  (9) Spiracle, striate impression, and fovea of 5th abdominal segment.
  (10) Lateral view ; the operculum also shown extended.
  (11) Prothoracic legs.
  (12) Left mandible, external view.
  (13) Labrum.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Early stages of two species of *SANDALIDAE*.

ON THE STRUCTURE OF THE COMPOUND EYE OF *ALEURODES BRASSICAE*, WALK. (HEMIPTERA)

By H. Eltringham, M.A., D.Sc., F.R.S.

[Read 6th May, 1931.]

Plate XXV.

Some considerable time ago my friend Dr. C. B. Williams drew my attention to the peculiar arrangement and pigmentation of the corneal lenses of the compound eyes of *Aleurodes brassicae* and suggested that I should investigate their histological structure. Scarcity of material at the time and pressure of other work prevented my dealing with the matter until recently. Meanwhile Dr. Williams gave an excellent account of the external features of the *Aleurodes* eye at a meeting of the Entomological Society on June 18th, 1930, and the report of his observations will be found in the *Proceedings* **5** : 56.*

The compound eye of the insect is externally divided into an upper and lower portion. The extent of this division varies considerably in related species, being in some incomplete, while in others there is rather wide separation. The special feature of the cornea, to which Dr. Williams called attention, is the curious fact that the lenses are arranged in groups of seven, of which six are pigmented and lie in rosette formation round the seventh, which is entirely unpigmented. The six coloured lenses are deep yellow, while the seventh is quite colourless. This arrangement is very regular in the lower half of the eye, but less so in the upper half, in which two or more unpigmented lenses are sometimes contiguous. The appearance of a part of the cornea of the lower eye is shown in Plate XXV, fig. 4, which was drawn with the reflector and a twelfth-inch oil-immersion objective. The accompanying text-figure is a reproduction of a microphotograph taken by Dr. C. B. Williams.

The facets are laterally compressed into rather irregular hexagons. The present investigation has been concentrated on the structure of the lower eye, though except for the fact that its facets are rather larger, the ommatidial structure appears to be the same in both lower and upper divisions. The ommatidia of both upper and lower eyes are curved towards one another beneath the cuticle, and become contiguous where they join the brain.

In both divisions the corneal surface is rather flat. The upper eye is directed forwards and upwards and the lower eye downwards. There are in addition two ocelli, more or less dorsal and posteriorly adjacent to the upper eye.

The external appearance of the compound eyes is shown in Pl. XXV, fig. 1, which represents them as seen by reflected light with the head slightly flattened under a cover slip. They are similar in both sexes. One of the most striking features is the small size of the ommatidia in comparison with the external area of the eye. They are embedded in a disproportionately massive layer of deep red pigment, and since the lenses cannot be easily distinguished in a surface view, the general appearance suggests a regular series of rather widely separated holes in a fine sponge.

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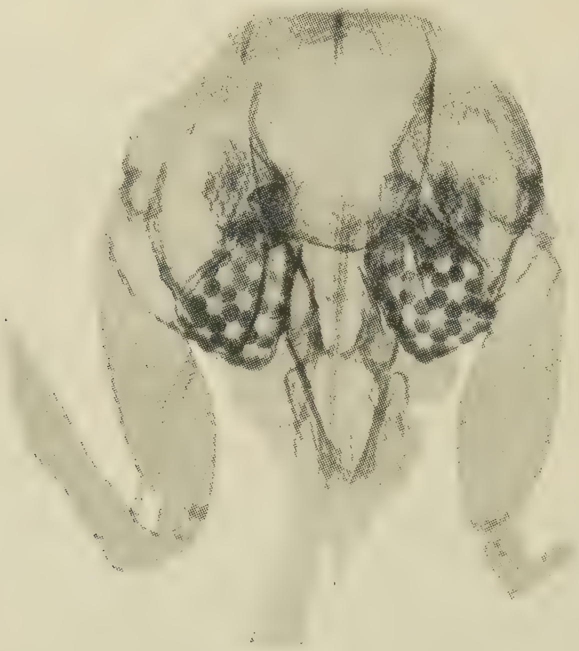
* I regret that by a misprint in *Proc. Ent. Soc. Lond.* **6** : 25 Dr. P. A. Buxton's name was substituted for that of Dr. Williams.

Pl. XXV, fig. 2 is a reflector drawing of a section passing through the long axes of the two lower eyes. Their diverging angles and a considerable curvature in the ommatidia combine to cause much difficulty in orientation for embedding, difficulties which are further increased by the small size of the eye, which is only about ·07 mm. in diameter. I have found saffranin and light green an excellent compound stain for these sections, since the pigmented lenses take a rich scarlet and the colourless lenses a pale blue green. Depigmentation of the sections is essential and very slow, 24 hours in Grenacher's fluid scarcely sufficing to remove enough of the red colour to enable the rhabdoms to be distinguished from the large pigment cells. In the section, Pl. XXV, fig. 2, *B* is the brain substance, *L* the lower eye, *upl* an unpigmented lens, *pl* a pigmented lens, and *m* muscle fibres. A semi-diagrammatic view of the lower eye is shown in Fig. 3, where *upl* is an unpigmented lens, *pl* a pigmented lens, *pc* a pigment cell, *rh* a rhabdom, *bm* the very elementary basement membrane, *pn* the perceptive nerve layer, and *gbs* the finely granulated brain substance. Beneath the lenses there are distinct cones exhibiting well-developed " Semper's " nuclei. Judging by their softness and slight resistance to distortion I consider them to be of the type known as pseudocones, *i.e.* of a fluid rather than of a chitinous nature. If I am correct in this assumption these eyes are exceptional in Hemiptera, since Weber (*Biol. d. Hemipteren*, 1930, p. 117) states that pseudocones are unknown in this order, though he adds that the eyes of *Aleurodes* had not, at the time of writing, been histologically examined.



Microphotograph of Head of *Aleurodes*.

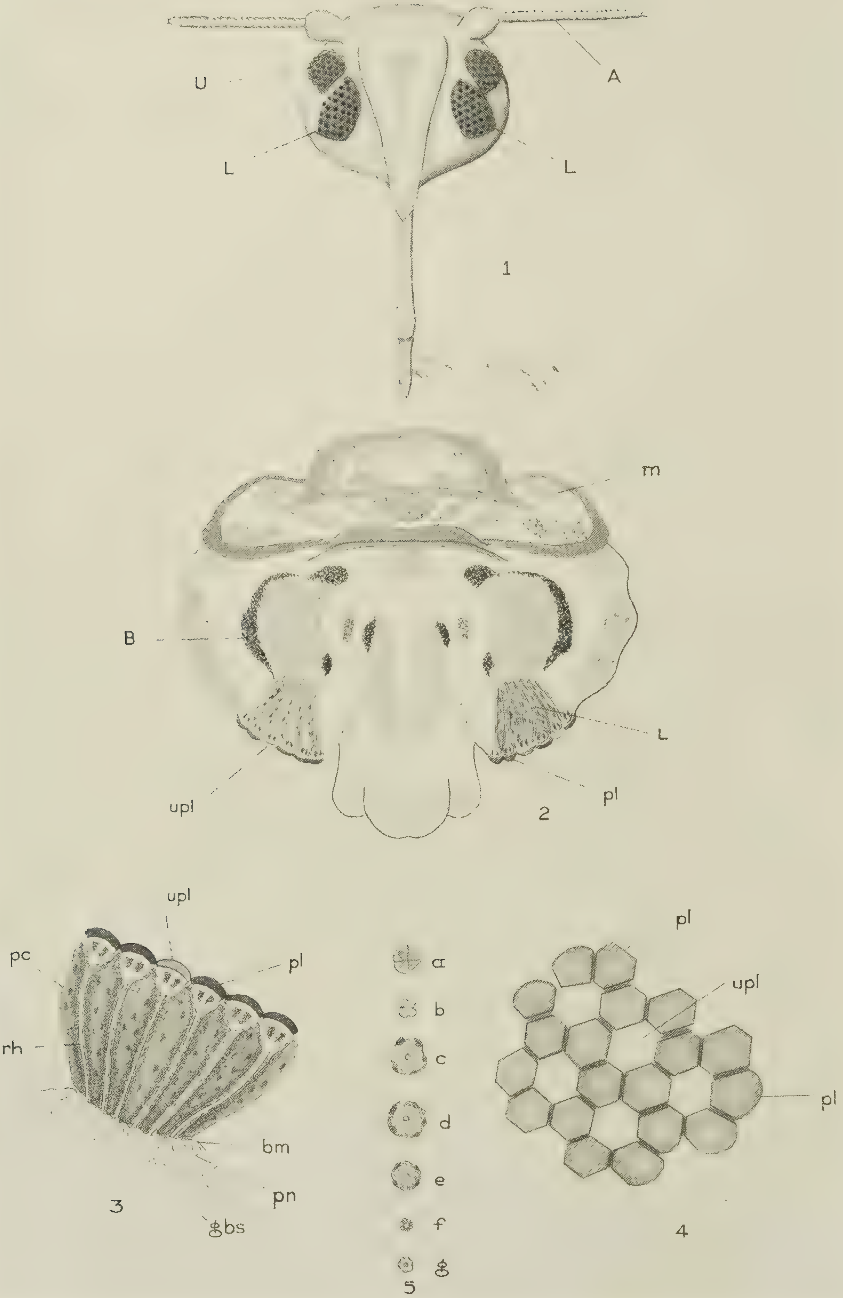
In the majority of insect eyes the rhabdom is surrounded by retinulae, special nerve endings extending from the periopticon to, or nearly to, the apices of the cones. Where the combined action of the corneal lens and the so-called crystalline cone produces an actual erect image at the cone apex, these retinulae are capable, as I have shown for the eyes of butterflies (*Trans. Ent. Soc.*, 1919), of acting as the perceptive elements, and where, as in *V. urticae*, they are numerous, they must considerably increase the acuity of the insect's vision. In none of my longitudinal sections of the eye of *Aleurodes* can any retinulae be seen. Indeed, I was for some time under the impression that they did not exist. Fig. 3 shows all that can be seen in such a section, even with a twelfth-inch oil-immersion objective. The rhabdoms are of very slightly smaller diameter at the proximal than at the distal end, but there is no evidence of that thickening, due to the bundle of retinulae, so evident in the majority of insect eye sections. By preparing very thin transverse sections, staining them green, and examining them by a red light under the highest magnification, I was, however, able ultimately to detect the presence, in a part at least of the ommatidium, of minute nerve fibres. Fig. 5, *a* to *g*, represents the successive appearances of a series of transverse sections. At *a* the cone is divided into the usual four cells. At *b* it is becoming narrower and the cell divisions are less obvious. At *c*, *d*, and *e* the rhabdom is surrounded by the great mass of pigment cells with their nuclei. Near the proximal end of the ommatidium we see the appearance shown at *f*, and here there seems no doubt that the rhabdom, represented by the small central circle, is surrounded by eight minute nerves. Micrometer measurements of these give a diameter of the order of about ·0007 mm. They can be detected in about three sections (of approximately ·002 mm. thick) and then become indistinguishable, the subsequent appearance of the ommatidium being shown at *g*. From these sections we must assume that the rhabdom at its base is embedded in a single nerve thread, which, arising from the preceptive layer (*pn*, Fig. 3), passes through the basement membrane and soon afterwards divides into eight delicate nerve endings which travel upwards for a very short distance. The whole structure is of an extremely primitive kind, and there is no trace of the basement layer of large nerve cells, the fibre bundles passing to the periopticon, the trachaeal distributors, or other structures found in more highly developed eyes.

We may now ask, in what respect do the unpigmented lenses in the proportion of one to two, differ, optically, from the pigmented lenses. They are of slightly smaller diameter, but a regular curve touching the outer surfaces of the pigmented lenses also touches the pigmented. Hence their external convexity must be slightly greater. Other factors being equal this would suggest a greater refractive power. On the other hand, the unpigmented lens, as shown by its reaction to staining methods, is of a lesser degree of chitinisation. That this property balances its greater convexity seems to be demonstrated by the following experiment. I succeeded in dissecting out and cleaning a great part of the cornea of the lower eye. It was then mounted on thin glass on a drop of very dilute glycerine and placed under the microscope with the external side downwards. After removal of the substage condenser, a steel rod, of about the thickness of a medium knitting-needle, was moved in a horizontal plane between the reflector and the stage of the microscope. The focus was then adjusted until the images of the rod formed by the corneal lenses could be distinctly seen. These images were equally well defined by both pigmented and unpigmented lenses, and focused at the same distance behind the proximal surface of the cornea.

There is a further complication from the optical point of view. The yellow lenses presumably cut off part of the blue end of the spectrum, while the uncoloured lenses admit the whole range of light rays. Now the yellow and infra-yellow rays are of less refrangibility than those beyond the yellow and extending to the blue, and as we cannot assume that the simple lenses of the cornea have any apochromatic correction, we should expect that the sharpest image obtainable would be rather nearer to the cornea in the case of the uncoloured lens if its optical refractive power were the same as those of the yellow lens. This does not appear to be so, and we are led to the conclusion that in spite of a different curvature, less chitinisation, and absence of pigment, the focal length of the uncoloured lenses is roughly the same as that of the yellow ones.

I have spoken of the *image* formed by these lenses. It must not be supposed, however, that the facet images, as such, are of any value in an eye of this simple character. Images are necessarily formed by the convex lenses of insects' eyes, but whether they are of any value for perception depends on the nature of the underlying structures. As I have shown (*l.c.*, *supra*) the lens and cone together in a butterfly's eye form a small erect image of the field of view of each facet. All these little erect pictures together form a complete erect picture adequately perceived by the numerous retinulae, of which there are in *urticae* eight to each facet. Some types of facet, as for instance those in the dragon-fly's eye, give a small inverted image, but this is not re-erected by the action of the cone, and hence it can be of no use as an image, since a mosaic of inverted images would not make an intelligible picture. In the dragon-fly's eye the inverted image is of use only as a spot of light having the average value of the light transmitted by its respective facet. All these spots of light together form an erect image of the whole field in the same way as a " half-tone " picture is represented by light and dark dots. This is one form of the " apposition image " of Exner. The " superposition image " of the same author is that found in the eyes of nocturnal and crepuscular insects which have movable pigment sleeves surrounding the apices of the cones. When the light is weak, the pigment moves forward so that more light passes out of the cone apices to the percipient layers. Under these circumstances part of the image of the field of view produced by each cone may overlap parts of the images produced by adjacent cones, and, assuming the " register " to be correct, the total resulting image is correspondingly better illuminated. The eye of the male glow-worm produces a very perfect image of this kind.

We are now in a position to estimate the nature of the image provided for the receptive elements in the minute eye of *Aleurodes*. The lower eye contains about 40 facets Its surface is very flat, and hence, in comparison with the more or less hemispherical eye of many insects, its field of view will be very small. This will be a considerable advantage, since widely radiating facets must be very numerous (as in the dragon-fly) if they are to cover their correspondingly wide field. In *Aleurodes* the advantage must be largely discounted by the small number of the facets. Apparently each facet produces a minute spot of light affecting an equally small area of the perceptive layer lying at the proximal end of the rhabdoms. There can be no superposition image even if there were any suitable nerve apparatus to perceive it, since the pigment cells are dense and immovable. The retinulae are very small and do not extend far along the rhabdoms. The depth and extreme density of the pigment probably assists the small quantity of light admitted by establishing a powerful contrast, just as we can see a very faint light more easily in dark surroundings. Never-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Eye of *Aleurodes Brassicae,* Walk.

theless the image received must be ill defined and feebly illuminated except at very close range. Actual experiment shows that the creature is conscious of a small moving object at a distance of about one-sixteenth of an inch. If a sufficient number of facets are engaged at this distance to perceive such an object, we must remember that the number of facets engaged in viewing an object of constant size is inversely proportional to the square of the distance, and therefore at twice the distance only one-quarter of that number of facets will be engaged. Hence at one-quarter of an inch, or four times the distance, the insect could hardly be said to see at all. Even adding the effect of the upper half of the eye to that of the lower its range and acuity of vision must be exceedingly small.

Whilst these considerations may contribute to an estimate of the nature and extent of the insect's visual powers, they do not, as I am aware, offer any explanation of the purpose or effect of the curious distribution of the pigmented and unpigmented lenses, nor do I feel able to offer any suggestion which would throw light on the matter. *A. brassicae* haunts the undersides of cabbage leaves. It is of rather sedentary habits, though doubtless uses its wings when migrating to fresh pastures. If we look at a landscape through a yellow light-filter all the greens are somewhat accentuated. Its yellow vision may help it to find green things more easily. Lloyd (*Bull. Ent. Res.*, **12** : 355, 1921) finds that the species *A. vaporariorum* is powerfully attracted to yellow light. With its yellow eyes, light of that colour may be to it the brightest kind of light and this tendency merely a form of positive phototropism. There is still the question of the use of the uncoloured lenses. Perhaps a small proportion of unfiltered light may be of advantage for directional purposes when flying. On the whole, however I must regretfully admit that the reason for the remarkable structure remains, for the present at least, unsolved.

EXPLANATION OF PLATE XXV.

FIG. 1. Head of *Aleurodes brassicae* as seen by reflected light and slightly compressed under a cover-slip. *A*, part of antenna, *U*, upper half of compound eye. *L*,*L*, lower eyes.

2. Section through head of same. *m*, muscle fibres. *B*, brain. *pl*, pigmented lens of lower eye. *upl*, unpigmented ditto. *L*, lower eye.

3. Semidiagrammatic section of lower eye. *upl*, unpigmented lens. *pl*, pigmented ditto. *pc*, a pigment cell. *rh*, a rhabdom. *bm*, basement membrane. *pn*, perceptive nerve layer. *gbs*, granulated brain substance.

4. Surface view of part of cornea of lower eye, showing " rosette " formation. *pl*, pigmented lenses. *upl*, unpigmented ditto.

5. *a* to *g*. A series of transverse sections of an ommatidium. *a*, *b*, the cone. *c* to *e*, large pigment cells surrounding the rhabdom. *f*, the minute nerve endings or retinulae, surrounding the rhabdom not far from its base. *g*, the ommatidium close to the basement membrane. The separate nerve fibres appear to fuse into a ring enveloping the rhabdom.

AN ABNORMALITY OF PATTERN IN LARVAE OF *MAMESTRA PISI*, L.

By E. A. Cockayne, D.M., F.R.C.P.

[Read 3rd June, 1931.]

With Plate XXVI.

At the end of September 1930 larvae of *Mamestra pisi* were very abundant on the broom in one corner of Barnes Common. Amongst them I found more than sixty with an abnormality of pattern, and Mr. C. N. Hawkins found others in the same place a few days later. I estimate that at least one in twenty was affected in this restricted area. Twice I found two abnormal larvae on the same shoot, and once I found three close together on a bigger stem. It was quite a common event to see more than one such larva on the same bush.

In no case was there any error of segmentation or scarring of the skin, and in only four was there an associated anomaly, the absence or reduction in size of one or more spiracles. The very large larva (Pl. XXVI, fig. 9) taken by Mr. Hawkins has no spiracle on the fourth and fifth abdominal somites on the right side, and the last spiracle on the left side is missing in two larvae (figs. 20 and 21). One larva (fig. 14) has a very small functionless spiracle on the fifth abdominal somite on the left side. In all these four larvae the absence or small size of a spiracle coincides with a derangement of pattern.

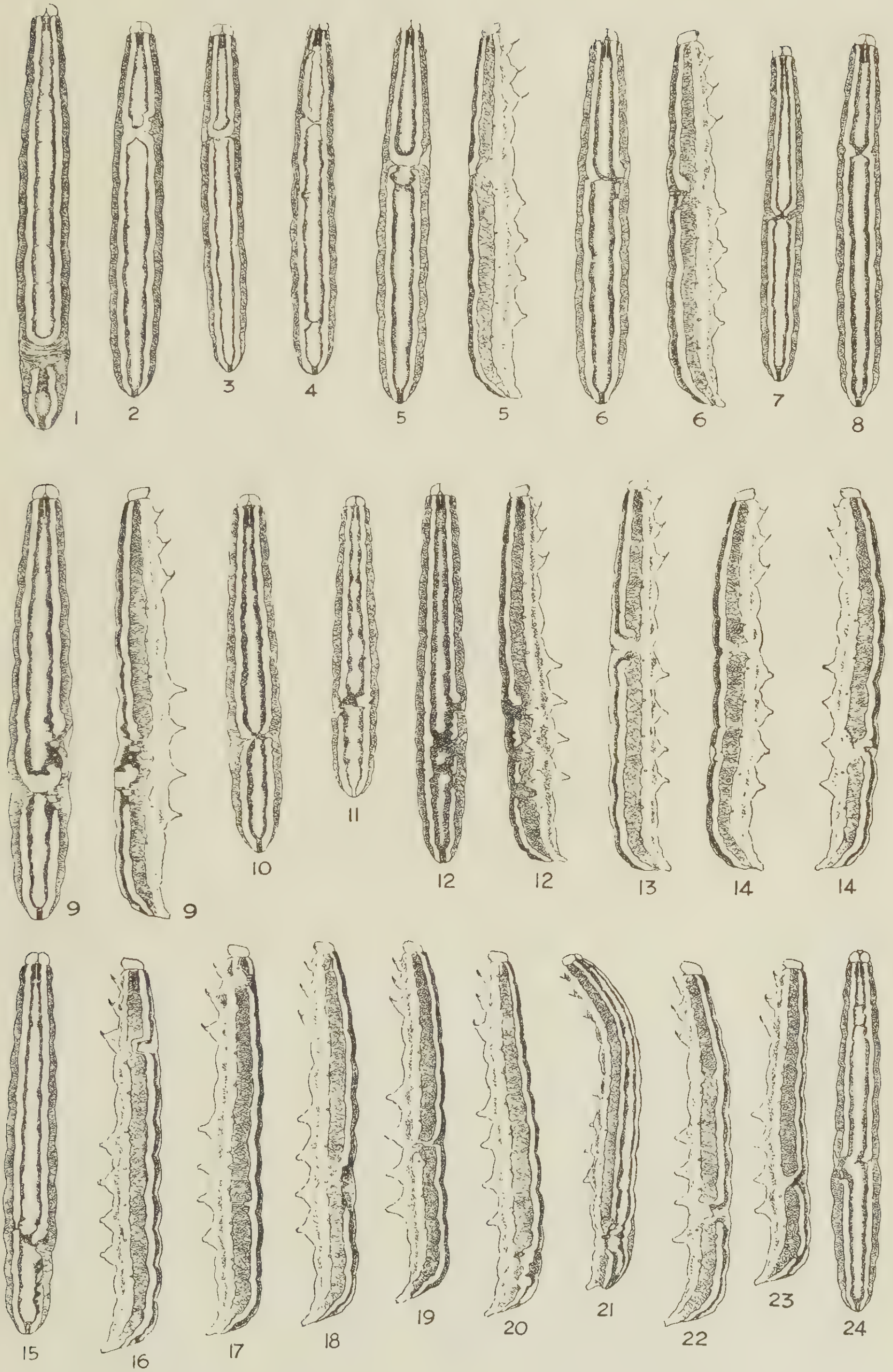
The abnormality of pattern itself follows a definite plan, so that, though no two larvae are exactly alike, an individual can often be closely matched by another. For instance, those shown in figs. 6 and 24 are very much alike and there are two more with almost the same dorsal pattern, and there is another very similar to that shown in fig. 16. The scheme of the altered pattern is a tendency for the two yellow subdorsal lines to unite and form a loop on the dorsum, and in six there is a complete union with the formation of a perfect loop in five of them. Examples of this are shown in figs. 1, 2, 3, 4, 5, and 9. There is also a tendency for the one yellow subdorsal line to unite with the yellow lateral line of the same side, and complete union of these two lines is found in several larvae, as in those shown in figs. 14, 19, 22, and 23. In a number of larvae there is either a tendency for the two subdorsal lines to unite or an actual union between them, and also an attempted junction between a subdorsal line and a lateral line on the same somite, as in those shown in figs. 3, 5, 6, 9, 11, 12, 13, 14, and 24. In many larvae in which the subdorsal lines do not unite the dark markings internal to them are extended right across the dorsal surface. This arrangement is seen in figs. 6, 7, 8, 10, 11, 12, and 15. In others, however, these dark markings are deficient or absent at such a point as can be seen in fig. 16 and in fig. 14 on the right side. Where there is an attempt at the formation of a junction between a subdorsal and a lateral line, the subdorsal is often broken or narrowed as many of the figures show, and less frequently a similar breach occurs in the lateral line as in figs. 6 and 19. In some larvae with a complete or incomplete lateral loop the fine striae defining the lower margin of the lateral line are absent as figs. 9, 13, 14, and 22 illustrate, and when there is a breach in a subdorsal line the striae beneath may spread into it, and in one larva, fig. 1, the striae of both sides unite on the dorsum behind a perfect subdorsal loop.

Any somite may be affected, and in several larvae more than one somite is abnormal; in some the abnormal somites are adjacent, and in others they are widely separated. The larva shown in fig. 4 has the subdorsal lines displaced on the first thoracic and first, second and eighth abdominal somites, and the lateral line on the right side of the second thoracic somite nearly joins the subdorsal. That shown in fig. 14 has an incomplete lateral loop on the right side of the second and a complete lateral loop on the left side of the fifth abdominal.

The larvae least affected merely have a small gap in the subdorsal line or a wedge of yellow colour extending inwards or outwards from it, as in the eighth abdominal somite of that illustrated in fig. 23 or in the fifth of that illustrated in fig. 17.

All the larvae figured are from Barnes Common except fig. 11, which was found by Mr. H. B. Williams and myself near Esher in 1928. Mr. Hawkins found some like the less aberrant ones from Barnes on Wimbledon Common, and Mr. H. Worsley Wood tells me he has seen similar larvae on Barnes Common in previous years. Larvae with this peculiar alteration of pattern evidently occur regularly at Barnes, and they are probably widely spread over Surrey.

The numbers found close together and the high percentage in such a small area make it likely that there were several broods each containing a proportion of aberrant members. These facts and the deductions I have drawn from them can be explained most simply by supposing that the defect is an inherited mutation. If the abnormal pattern were due to injury one would expect to find scars and one would not expect it to conform with any regular plan. Mr. I. M. Montgomery, however, tells me that many years ago he found a larva of *Calocampa vetusta* pierced by a thorn in its penultimate instar, no cicatrix was visible in the last instar but two of the lines had coalesced at this point. If the pattern in the *pisi* larvae had been altered in this way, the injuries in some must have been large and in others numerous, and it is difficult to imagine how they could have happened on a plant so soft and smooth as broom, growing, as it was, away from any thorny plant. I hope to prove that my suggestion is correct by breeding from abnormal larvae, but in the case of a Noctuid this is difficult, and as I shall probably fail, and as even if I succeed I shall have no results to show for three years or more, I think it is advisable to put the facts on record now.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Abnormality of Pattern in Larval *Mamestra Pisi*, L.

A CONTRIBUTION TOWARDS THE STUDY OF THE GENERA OF THE EPIPASCHIINAE (FAMILY PYRALIDAE)

By A. J. T. Janse, D.Sc.

(Hon. Professor of Systematic Entomology, University of Pretoria; Government Research Scholar 1921.)

[Read 6th May, 1931.]

With Plates XXVII to XXXVII and Three Text-figures.

Acknowledgment.

In preparing this paper I am extremely obliged to the following gentlemen and Institutions for the loan and presentation of specimens, comparing types and in other ways assisting me :—

Mr. Joicey of the Hill Museum, Dr. W. Schaus, Mr. W. H. T. Tams, Mr. E. Meyrick, Sir George Kenrick, Messrs. Benjamin and McDunnough, Mr. Bethune-Baker, the Berlin Zoological Museum; to all I herewith offer my heartiest thanks.

My special thanks are due to the Board of the Carnegie Grant in Aid of Research for bearing the cost of reproducing all the illustrations.

Introduction.

Some time ago Dr. W. Schaus was kind enough to go over some of my unnamed Epipaschiinae, among which he found some new and interesting species, and these he kindly returned to me for description.

In order to make sure that each of these was placed in the right genus, a more detailed study was made of the genera than before, and the male sexual characters were especially studied with rather surprising results.

At first sight the characters and definitions given of the 48 genera described up to the time when the study was commenced, seemed to be fairly satisfactory if venation was used mainly for classification, but when other, often hidden, characters were taken into consideration it was found that this classification was often very unsatisfactory. The reason for this probably lies in the fact that the species of this subfamily show secondary sexual characters, which are very distinctive for the males but which are hidden or perhaps absent in the females, while the venation is far less differentiated. However, I strongly suspect the females to have corresponding organs or at least structures that are in one way or another influenced by such male organs, only they take a great deal of finding and are bound to escape such casual observation as the mere looking at the insect under a magnification of about ten times without dissecting a single part. It is on such observations that much lepidopterological classification is based and, if a great deal of the history of this group had not been preserved in the wing-venation, our present classification would still be very much in the state in which Hübner left it.

Several workers have taken the secondary characters of the males into consideration when defining a genus, and as a result a large number of genera have been formed solely on male characters. Other workers, especially that energetic worker Sir George Hampson, in his paper on this subfamily in the *Transactions of the Entomological Society of London*, **1896**: 453–478, lumped many of these genera on the strength of the fact that these characters are found in one sex only.

I certainly agree with the principle that a species is constituted of both sexes, and would even go so far as to state that a description given of one sex only is not a full description, is therefore worthless for defining the species, and should consequently not be recognised unless both sexes show the same characters and this fact is indicated in the original description. If such a rule could be passed, hasty and incomplete work, based on one specimen only, would be avoided and more sound work would be the result.

On the other hand, as this paper intends to show, male characters, even if secondary, are frequently of the greatest importance, and I feel sure that, if looked for, similar important characters can be found in the female, especially in the genital organs. Lack of time prevented me from making a thorough study of the females, but I certainly consider such study of the greatest importance and hope later on to be able to devote more time thereto.

The present paper thus deals mainly with the male characters, and my study of these has convinced me that they rank as high as, if not higher than, the study of venation. It has compelled me to restore many of the synonyms to their previous generic place.

Of these secondary organs the sexual organs of the males are of the greatest importance, not only in this group but in most others that have been studied by me from that point of view. I now consider them of so much importance, that I hold that they should always be taken into consideration, not only in defining the species but also in the limiting of a genus; in short, that a description without mention of them is most incomplete and should for that reason not be recognised.

The study of the genitalia requires, of course, the making of microscopic preparations, as one cannot see most of the details on ordinary dried specimens, and this method has the advantage that a more permanent record is kept of the observation, which can be studied by later workers, even if the original specimen were destroyed by museum pests. The same really holds for the microscopic study of palpi, antennae and legs, and, here too, I consider a microscopic slide to be the only satisfactory method for studying these structures in detail and preserving a permanent record, which can be used later on for verification.

All specimens studied for this group were dissected and the parts mounted in canada-balsam; the specimens from which the parts were taken were suitably labelled and preserved. In this way, the cabinet specimen, thus "mutilated," together with the microscopic slides, formed one unit for study. The genitalia were all studied laterally and from the dorso-ventral view, the whole abdomen being as a rule mounted laterally after the left valve was removed and the whole stained with fuchsin. The other parts were only cleared by means of xylol and mounted in balsam without staining, usually without removing hairs or scales, as the structural details were, as a rule, quite clear after a few days. In this way were seen and made use of structures which were bound to escape the casual observation mentioned before.

The male genitalia of the EPIPASCHIINAE are very characteristic, the scaphium being typical for this group, so much so, that a glance at them verifies the true position in the family, and some species, placed here by some workers, have been thrown out of this subfamily, at first on the strength of the genitalia and on further study also of other characters recognised by most workers.* Hulst in 1889 had already made use of the male genitalia to a small extent for defining genera in this group, although the only figure given of these organs is represented upside down. No other workers have, to my knowledge, made use of genitalia in this subfamily, and no extensive use has been made by any worker of a detailed study of other sexual characters found in the male throughout this group.

In this paper an attempt is made to do so, though lack of material has left a number of lacunae.

Dissections were made and studied of all available genotypes, preferably from the type locality, not only of the genera recognised by Hampson but also of those which he sinks as synonyms, and this study has enabled me to restore many of them to generic rank.

In studying the position of the maxillary palpi on the specimen under high power I have come to the conclusion that several of my figures *probably* represent them in an upside down position. Owing to the thick scaling it is in most cases extremely difficult to be certain about this. In the following cases I feel fairly certain that they have to be reversed :—Plate XXVIII, figs. 1*a*, 2, 3, 4, 7, 13, 21, 22, 23; Plate XXXV, figs. 1, 2, 3, 5, 6, 9, 12, 15.

Genus **Neopaschia.**

Neopaschia, Janse, Trans. Ent. Soc. Lond., **1922** : 20.

Type : *flavociliata* Janse.

Pl. XXVII, fig. 1; Pl. XXVIII, figs. 1, 1*a*.

This genus I placed before *Anartula*, Staud., in the original description, and, as only females are known so far, I have yet no reason to change this view, which I based mainly on venation, a character which *by itself* I now consider less reliable for the framing of a natural classification. Unfortunately the genotype of the genus *Anartula* is known to me in the female sex only, and I am thus unable to form a more definite opinion on the relationship of these two genera.

To the original description I can add, that the maxillary palpi, though minute, are well developed and probably consist of two joints, as shown in fig. 1*a*. There is, further, a possibility that vein 7 is in reality vein 8, as it terminates just at the place where that vein ends in *Anartula*. I am eagerly endeavouring to secure males of these two interesting genera.

Only one species is known so far.

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* A case in point was *Stericta* sp., represented in the B.M. collection by one specimen bearing a ms. name. None of my specimens showed clearly the required raised scales, and in general appearance it was also unlike a typical Epipaschiine. When the genitalia were prepared they proved to be unlike any of the hundreds of preparations examined, though as yet I could not place them in a particular group. A wing-preparation was then made and showed that vein 7 was not stalked with 8, 9, but ran very close to the stalk of 8, 9, so close indeed as to appear as if stalked when the scales were still on. It thus belonged to Hampson's group HYDROCAMPINAE, SCOPARIINAE, PYRAUSTINAE. As vein 10 was free, it could be only one of the last two, and, as the raised scales were hardly distinct, it pointed to PYRAUSTINAE, but the genitalia were not as they typically are in that group. The genitalia of over a dozen various Scopariids were prepared and it was found to be a typical Scopariid. When a closer study is made of that group, more information will be given about the true position of this species, but it was surprising to me, even after years of genitalia study, to find the genitalia of such sterling value in the classification of genera.

Neopaschia flavociliata, Janse, *loc. cit.*, p. 20.

Hab. Barberton, Three Sisters (Barberton Distr.), Transvaal.

Genus **Anartula.**

Anartula, Staud., 1893, Deuts.ent.Z. Iris, **5** : Pl. III, fig. 22 ; **6**, 78.
Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 454.
Holland & Schaus, 1925, Ann. Carnegie Mus., **16** : 55.
Parorthaga, Hmpsn., 1896, Fauna of Brit. India, Moths, **4** : 110.

Type : *melanophia*, Staud.

Whether *Anartula* and *Parorthaga* are the same I have not been able to decide as I have not seen Staudinger's original description, and I doubt whether this would throw any further light on the subject. It should be noted, however, that the descriptions given by Hampson for both genera are word for word the same without any exception, and the curious thing is, that the type of *Parorthaga* (*Balanotis euryptera*, Meyr.) was sunk as a synonym of *A. melanophia*, Staud., by Hampson in April 1896, but kept as a good species in October of the same year in his *Moths of India.*

The question now arises, from which species has the description been made, from the Siberian species or from the Indian one? Personally I doubt whether these two are co-specific, until I have compared the males from these two localities.

Description from *Anartula melanophia*, Staud. Pl. XXVII, fig. 2.

Unfortunately I have only a female in my collection, from Ceylon, identified by Hampson and provided with a label in Hampson's handwriting, but at that time placed by him in the genus *Lepidogma*. This, however, is quite wrong, seeing that veins 4,5 are distinctly stalked. This specimen agrees well with Hampson's description and key.

It should be noted that the Indian specimen (from Sambawa) was placed by Meyrick in the genus *Balanotis*, which he considered to belong to Pyralinae and not to Epipaschiinae. In my specimen vein 8 of hind-wing is distinctly anastomosing with 7, while the presence of erect scales is doubtful. The general appearance of this species would lead one to place it erroneously in the Pyralinae.

Maxillary palpi well developed, filiform and probably three-jointed. Hind legs with two pairs of spurs, outer spur shortest. The antennae of the male are supposed to be without a process and the fore-wing to have a costal swelling.

Genus **Oneida.**

Oneida, Hulst., 1889, Ent. Amer., **3** : 130; **5** : 63.
Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 455. (Here given as a synonym of *Tioga.*)

Type : *lunulalis*, Hulst.

Description from *luniferella*, Hulst.

My specimen has an old label identifying it as *lunulalis*, but also another label, by Barnes and McDunnough, stating it to be *luniferella*. On comparing it with Holland and Schaus' figure, there is no doubt about the latter identification being correct.

In later ms. work Hampson considers *Oneida* a good genus and perhaps rightly so, for all the veins of the fore-wing are present in *Oneida*, while vein 10 is missing in *Tioga*. The spurs cannot be taken as differing from *Tioga*, however, for Hulst states that the male has end spurs only, while the female has two pairs of spurs. I should not be surprised if the male has normally two pairs also and that the type specimen was either an abnormality or a "museum specimen." Unfortunately my specimen is the latter, as it has no legs at all, so I cannot verify the normal condition. The labial and maxillary palpi are very similar to those of *Tallula atrifascialis* and *Tioga aplastella*. Unfortunately I have a male of *luniferella* only, so that I cannot compare the genitalia of the three species. I also expect to find generic differences, however, though no doubt they come very close together.

Oneida luniferella, Hulst.

1895, Canad. Ent., **27** : 53.

Pl. XXVII, fig. 3; Pl. XXVIII, figs. 2, 2*a*; Pl. XXX, fig. 1; Pl. XXXI, fig. 1.

As will be seen from the illustrations the labial palpus is peculiar for its rather long and slender third joint, while the maxillary palpi are large enough to be seen with a good hand-lens and not invisible, as Hulst states; the process of the antennae is not longer than usual, as Hulst states, though it is fairly well developed.

Hab. Canada.

In addition to the type the following species should also be included here according to Dr. Schaus :—

Oneida mejona, Schaus, 1922, Proc. Ent. Soc. Wash., **24** : 209.

Hab. Volcan, Santa Maria; Guatemala.

Genus **Plutopaschia.**

Plutopaschia, Hmpsn., 1917, Ann. Mag. Nat. Hist., (8) **19** : 361.

Type : *Stericta sinapis*, Roths.

This genus and its type are only known to me from description.

Plutopaschia sinapis, Roths. Rep. B.O.U. Exp. Dutch New Guinea 2, No. 15, p. 115, fig. 64 (1916).

Hab. New Guinea.

Genus **Tioga.**

Tioga, Hulst, 1889, Ent. Amer., **4** : 113 (1888). Ent. Amer., **5** : 69.
Hmpsn., **1896**: Trans. Ent. Soc. Lond., 455.

Type : *aplastella*, Hulst.

Description from *atrifascialis*, Hulst.

Pl. XXVII, fig. 5; Pl. XXVIII, fig. 4; Pl. XXX, fig. 2.

The type of this genus, *T. aplastella*, Hulst, is unknown to me and was not known to Hampson either, though in ms. notes made by him it is stated that according to Dyar this species and *Pococera militella*, Zell., would be the same. This view, however, is not followed by Holland and Schaus (*l.c.*, p. 57), where *militella* is kept in the genus *Tetralopha*, which was made a subdivision of *Pococera* by Hampson. This worker as well as Holland and Schaus kept *atrifascialis* in this genus. Of this species I have a specimen of undoubted identification, so I use *atrifascialis* for the description and figuring.

According to Hampson the difference between the two genera is as follows :—

Tioga.	*Pococera.*
Palpi reaching *well* above vertex of head.	Palpi with end of *second joint just* above vertex of head.
Tibia slightly hairy.	Tibia smoothly scaled.
Fore-wing with vein 3 from angle of cell; 6, 7, 8, 9 stalked; 10 free.	Fore-wing with vein 3 from below angle of cell (according to figure); 6 free; 7, 8, 9, 10 stalked.
Hind-wing with 6, 7 stalked.	Hind-wing with 6, 7 from upper angle.

Of these characters the stalking of 10 with 7, 8, 9, in *Pococera*, or the stalking of 6, 7, 8, 9, in *Tioga*, may be taken as the most important character, but even that *by itself* is not reliable, when the stalking in the one genus is very short and in the other these veins come from a point, as is the case in veins 6, 7 of the hind-wing. Only when these characters coincide with other characters as well, such as *structure* of palpi and genitalia, can we regard these as of sufficient value. Unfortunately many workers give no attention to structure, but only mention position and relative length of palpi, as seen when covered with scales, and the real structure of these organs remains hidden.

In my specimen the fore-wing has veins 3, 4, 5 closely approximated to one another and 4, 5 approximated for a long distance; this made Hulst think (*l.c.*, p. 72) that they were stalked, which is certainly not so. This character is just indicated in Hampson's figure, but not made use of in the description and treated as if of no importance, while in other groups this character is largely used by him for separating genera, otherwise closely resembling one another.

It is quite possible that further study of genotype material will prove that *Tioga* should be merged into *Pococera.* In the male genitalia there is no essential difference; only the shape of the valve is a little modified.

Twelve species have been placed in this genus by Holland and Schaus, all confined to America.

Macalla mira, Druce, was placed by Hampson, according to his ms. work and the B.M. collection, in this genus, while Holland and Schaus (*l.c.*, p. 101) place it in *Jocara.* They had only a female specimen, the figure of which agrees well with the male type, which is in my collection. The general appearance misplaces this species in *Tioga*, though the palpi, especially the maxillary palpi, somewhat agree. It is certainly wrongly placed in *Jocara*, as I define this genus, but further study of the genitalia will have to decide, and for this I do not as yet feel justified in using the type.

Genus **Pococera.**

Pococera, Zell., 1848, Isis, **1848** : 874.
Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 456.

Type : *gibella*, Zell.

Pl. XXVII, fig. 6; Pl. XXVIII, figs. 5, 7; Pl. XXXI, figs. 2–5.

Of *gibella*, Zell., I have seen two specimens, male and female, kindly sent to me for study by the Berlin Zoological Museum; no American museum seems to have this species, and Hampson states that it is also not in the Brit. Mus., so I have no means of verifying the identification.

It is peculiar that both these specimens have a venation in the fore-wings different from that given by Hampson, who also gives *militella* (the type of

Tetralopha) as the figure for *Pococera*. Unfortunately the male I have before me is without a head, so that I am not able to study the male palpi of this species.

In the male vein 11 of fore-wing is stalked with 12 for more than half its length, and in the female vein 11 comes from the upper median some distance from upper angle and then anastomoses with 12 for some distance. I assume that this is the way vein 11 got stalked in the male, the basal half having disappeared (Pl. XXVII, figs. 6, 6*a*).

The stalking of vein 3, 4, 5 in fore-wing of male and of 4, 5 only in the female is also a good example of the unreliability of this character.

In *P. atromentalis*, Led. (Pl. XXVII, fig. 6*c*), and in *albimedialis*, Hmpsn. (Pl. XXVII, fig. 6*e*), the costal part of the fore-wing is rather deformed, and in the former vein 11 just touches vein 12 at about two-thirds, while in the latter the stalk of 7, 8, 9, 10, and vein 11 are curved to one another. In *P. fabianalis*, Schaus, that part is normal. In *albimedialis* veins 4 and 5 of fore-wing are remote and not stalked as in the others, but judging from the palpi I think this species should come in *Jocara*.

The typical palpi of *Pococera* I consider to be as in Pl. XXVIII, figs. 5 and 7, and I wonder if these coincide with the palpi of *gibella*. In *albimedialis* both labial and maxillary palpi are totally different and are just like those of some species of *Jocara*, and so are the antennal process and the venation of both wings, except for the contortion in the fore-wing.

According to Hampson's key the difference between *Jocara* and *Pococera* would be that the latter has vein 4, 5 of hind-wing stalked, while in the former they are supposed to be remote. In *J. trabalis* and in *J. rufiapicalis* they are stalked; in *J. basiochrealis* slightly stalked; in *ferrifusalis* from a point; in *argentilinea* approximate; in *sara* and *hispida* these veins are remote, so I fear that this is a very unreliable character. I further see no reason for keeping *albimedialis* in *Pococera* according to genitalia, as they resemble even better those of *Jocara*. I therefore remove this species to *Jocara*, mainly on the structure of palpi and antennae, seeing how artificial the classification is, when only based on the stalking or non-stalking of these veins.

The genitalia of the three species figured (Pl. XXXI, figs. 2, 3, 4) show no specialities, though it is peculiar that *atromentalis* and *fabianalis* have the valves rounded at the apex, while in *gibella* these are more pointed.

I leave it to future study to show what other species will have to come in this genus and which will have to be removed from it when the structure of the palpi of the male genotype is better known. These I expect to be as follows :—labial palpi not hollow, upturned, well above vertex of head, slender and covered mainly with hairs, second joint over twice as long as joint one, third joint as long as first, acuminate and with a sensory cavity at base; maxillary palpi filiform, three-jointed, about as long as first joint of labial palpus, covered with short hairs and scales.

Genus **Tetralopha.**

Tetralopha, Zell., 1848, Isis, **1848** : 879.
Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 456.
Holland & Schaus, 1925, Ann. Carnegie Mus., **16** : 60.

Type : *militella*, Zell.

This genus was sunk as a synonym of *Pococera* by Hampson, probably on account of the differences having been found by him in the male only. I do not agree with this principle, holding that special male structures must demand corresponding, though perhaps not homologous female structures, whether we can find them or not.

P. militella and *P. asperatella* are, according to Hampson, considered by Dyar as the same species and in his ms. notes he makes the change accordingly. Holland and Schaus still keep them separate, placing both species in *Tetralopha.* I have a female identified by Dr. Schaus as *T. asperatella*, which agrees well with his figure on Pl. XXXI, fig. 8, so I follow that view and consider my specimen to be *asperatella*, from which I make the figures. Unfortunately I have only a female.

According to Hampson the difference between this genus and *Pococera* and other allied genera is as follows :—

1*a*. Antennae of male without a process; fore-wing without furrow; veins 4, 5 stalked . . . . *Pococera.*
b. Antennae of male with a process from the basal joint; a deep furrow in cell of fore-wing above 2
2*a*. Fore-wing with veins 4, 5 from cell 3
b. Fore-wing with veins 4, 5 stalked . . . . *Wanda.*
3*a*. Fore-wing of male with a fringe of scales on basal half of costa below *Tetralopha.*
b. Fore-wing with no fringe of such scales . . . . *Auradisa.*

Pl. XXVII, figs. 4, 6*b*; Pl. XXVIII, fig. 3.

Whether the venation given in the plate is different from that of the male I do not know, but it agrees in all respects with that given by Hampson of *militella.* The same holds for the palpi, as far as can be made out from the small illustration and the description. A peculiarity in my specimen is the rather long and acuminate third joint of the labial palpi, which is about half the length of the second joint and the tendency in the maxillary palpi to bifurcate. Perhaps the latter character may be more pronounced in the male.

The genus seems to be confined to America, where it has about 50 species.

Genus **Auradisa.**

Auradisa, Wlk., 1865, List Lep. Ins., B.M., **34** : 1504.
Hmpsn. (as synonym of *Pococera*), Trans. Ent. Soc. Lond., **1896** : 497.
Holland & Schaus, 1925, Ann. Carnegie Mus., **16** : 74.

Type : *gelidalis*, Wlk.

As indicated in the key, the only difference between this genus and *Tetralopha* is the absence of a fringe of scales on the costa of the fore-wing in the male. As I do not know the genotype, I cannot say whether there are other differences as well. I suspect that there will be and the question will have to be settled after further study. Holland and Schaus keep it as a valid genus, but do not give any reasons. They include 17 species in it, while Hampson places as many as 20 species in this group, dividing them into another five subdivisions, all based on male characters. Even (*Macalla*) *viridis*, Druce, is placed here by him, which I certainly think is wrong (though it may prove not to be a *Macalla* either); as I have only two specimens of this species, of which the male is the type, I do not care to dissect it yet for detailed study.

Pococera metaxanthalis, Hmpsn., certainly is not a *Pococera*, but possibly a *Tancoa*, as is stated also by Holland and Schaus, *l.c.*, p. 79. I have only one female of that species in my collection, so I cannot make sure, but the general appearance certainly points to it.

Genus **Tancoa.**

Tancoa, Schaus., 1922, Proc. Ent. Soc. Wash., **24** : 217.
Holland & Schaus, 1925, Ann. Carnegie Mus., **16** : 77.

Type : *calitas*, Druce.

Pl. XXVII, fig. 7; Pl. XXVIII, figs. 8–11; Pl. XXX, figs. 3–6; Pl. XXXI, figs. 6–10.

The genotype is only known to me from the description and figure, but largely resembles *P. metaxanthalis*, Hmpsn., and I have quite a number of other species, which certainly belong here.

There is no doubt in my mind that this is a good genus. The shape of the wings is very characteristic, but the structure of palpi, antennae and genitalia place it in a group of its own, without any affinity known to me. Dr. Schaus also expresses this view, which he bases on the absence of vein 9.

The venation (Pl. XXVII, fig. 7) is as in the original description of *attenualis* with this difference, that veins 6, 7 of hind-wing are shortly stalked.

The palpi (Pl. XXVIII, figs. 8–11) are very peculiar in this group. The labial palpi are hollow, to receive the brush-like maxillary palpi; in *attenualis* the third joint is apparently absent; in all species studied the second joint is long. Maxillary palpi probably three-jointed, last joint very long and provided with long brush-like hairs. Antennae with small blunt process. Genitalia (Pl. XXXI, figs. 6, 7, 8, 9, 10) are very peculiar and would place *Tancoa* in a group by itself. Uncus multifid, flat and leaf-like; scaphium normal; valves with a projection from tip of upper margin, which probably in each species has a distinctive shape; penis simple.

It is possible that *Tioga mira*, Druce, has to be placed in *Tancoa*, though the genitalia will have to decide. The palpi are not as in *Tancoa*, but the fore-wing has also vein 9 missing; 6, 7, 8 are stalked, 10 is free. Hind-wing has 4, 5 well stalked.

Apart from the ten species placed by Holland and Schaus in this genus I also refer here the following species, which have been examined by Dr. Schaus, who agrees with me that they are undescribed.

Tancoa schausi, sp. n.

Pl. XXVIII, fig. 11; Pl. XXX, fig. 6; Pl. XXXI, fig. 8.

Resembles *T. crinita*, Schaus, in many respects, though it is slightly bigger; the postmedial line of fore-wing is evenly curved and less sharply defined, while the hind-wing of the male has a lighter colour. ♂ ♀. Fore-wing bronzy brown with a tinge of pinkish before medial and postmedial lines; basal area tinged with a greenish shade; medial line erect, slightly curved at medial fold, fuscous and preceded by a pale line of ground-colour; an oblique fuscous clouding from base of medial to top of postmedial lines; a well-defined, fuscous-black lunule at end of cell; postmedial line evenly curved from beyond two-thirds of costa to anal angle, of light ground-colour and preceded by a fuscous shading; terminal line consists of a series of fuscous-black elongate spots, broadest near apex; cilia brownish.

Hind-wing in male semi-transparent, irrorated with fuscous at outer margin; in female clouded with fuscous over the whole area; head, thorax and abdomen light brown, irrorated with fuscous. Antennae of male biciliate with cilia over one; in female simple.

Exp. in male, 27 mm.; in female, 29 mm.

Hab. Santo Domingo (S.E. Peru), 6000 ft., Nov. 1904, collected by Ockenden; one male, Rio Siato slopes of Choco (Colombia), 5200 ft. Sept. 1909; one female from Quinton, Carabaya (Peru), 5000 ft. Jan. 1905 (*Ockenden*).

Besides the types there are four cotype males and two cotype females.

Types in coll. Janse. One male and female cotype in Washington Mus.

Tancoa sinuata, sp. n.

Pl. XXX, fig. 5; Pl. XXVIII, fig. 10; Pl. XXXI, fig. 10.

This species resembles *attenualis* in colour, marking and size. Only the orbicular is more pronounced and entirely surrounded by a light-coloured ring; the postmedial begins further from the apex and is more oblique to vein 5, forming there a longer projected tooth, continuing to vein 3 and then almost erect to anal angle, *before* which it comes to the inner margin. In the fore-wing vein 10 comes from the stalk at the same place as vein 7, but perhaps this is an abnormality, for well below it is a swelling in the stalk and a slight dividing line, indicating imperfect union of the two veins.

The antennal process is a little longer and more pointed; the labial palpus is somewhat closed at upper half of second joint; the third joint of the maxillary palpus is much longer and of different shape. In the genitalia the valve has a different shape, especially towards apex; the apical process is narrower and of different shape; the uncus has differently shaped processes.

Although this is based on one male specimen only and generally looks very much like *attenualis*, I have no doubt that it is distinct.

Exp. 23 mm.

Hab. La Cambre (Honduras), 28 Jan. 1922 (*J. Lienhart*).

Type in coll. Janse.

Genus **Eutrichocera.**

Eutrichocera, Hmpsn., 1904, Ann. Mag. Nat. Hist. (7) **14** : 182.

Type : *paurolepidalis*, Hmpsn.

This genus is not known to me from specimens.

The genotype occurs in Abaco (Bahamas).

Genus **Calybitia.**

Calybitia, Schaus, 1922, Proc. Ent. Soc. Wash., **24** : 220.

Type : *picata*, Schaus.

Pl. XXVIII, fig. 8.

Only one male specimen of *C. picata*, Schaus, is in my collection, kindly presented to me by Dr. Schaus and provided with his identification label. Unfortunately this specimen is without a head, so that I cannot form an opinion about the structure of the palpi, which Dr. Schaus states to be very long, reaching beyond middle of thorax; the process of antennae is also said to be long and slender. The venation of my specimen is different from that given in the description; vein 10 is not stalked with 7, 8, 9, as stated, but runs so close to the stalk that its independent origin is difficult to observe; vein 6 is supposed to be from the upper angle, but here it is shortly stalked with 7, 8, 9; veins 4, 5 are supposed to be from lower angle, but my specimen has 4, 5 stalked for one-sixth.

The genitalia are practically the same as in *Oneida luniferella*, and so in fact is the venation; the valves are only slightly different in shape, such as would be found in another species of the same genus. The uncus is as in Pl. XXXI, figs. 2 and 11; valves as in Pl. XXXI, figs. 1 and 2. In general appearance the genitalia are as in Pl. XXXI, figs. 1, 2, 11, 12, 13.

I doubt whether this is a good genus, but future study of palpi and antennae must decide. The hind tibiae have median and terminal spurs.

Genus **Micropaschia.**

Micropaschia, Hmpsn., 1906, Ann. Mag. Nat. Hist., (7) **17** : 122.
Holland & Schaus, 1925, Ann. Carnegie Mus., **16** : 54.

Type : *orthogrammalis* Hmpsn.

Pl. XXVII, fig. 9; Pl. XXVIII, fig. 12; Pl. XXX, fig. 7; Pl. XXXI, fig. 11.

A specimen of the genotype was kindly identified and presented to me by Dr. Schaus and belongs to the same series mentioned by Hampson and Holland, namely those collected at St. Jean Maroni (Fr. Guiana). It further agrees very well with the figure given by Holland and Schaus (*l.c.*, Pl. 4, fig. 28). It also agrees with the *specific* description given by Hampson. I am thus quite sure that the *specific* identification is correct. In studying the structural characters, however, one would think it to be an entirely different genus as the principal characters, given by Hampson, are entirely different.

Unfortunately the head of my specimen was somewhat eaten, so that one labial palpus was missing, while in the preparation one maxillary palpus was lost; however, the remaining palpi were prepared on the slide and give full information. My specimen differs from Hampson's description in the following points :—Antennae of male with *short* cilia and shaft with narrow lamina at each joint; antennal process not covered with *hairs* but with *scales*; fore-wing with vein 2 from five-sixths of lower median; 3 from angle of cell (in the left wing *very* shortly stalked); 7 *absent*, coincident with 8 (the bending down of 7 and 8, as given by Hampson, adds to this puzzle; I do not see where that occurs). Hind-wing with vein 2 from three-fourths lower median; 3 *not* stalked with 4 and 5 but free, though at base there is a little approximation that may be mistaken for stalking, when the scales are left on; vein 4, 5 stalked; vein 6 *absent* (not stalked with 7, as Hampson gives); 7 anastomosing with 8 for about one-third of free part of 7 only and not too near apex, as Hampson has it.

I am at a loss to account satisfactorily for the differences mentioned and can attribute them only to two causes: either the venation is *very* inconstant or the observation made was hopelessly wrong. In the former case one asks what the value would be of a system so largely based on venation, if such differences can occur within the same species. Even though most workers will have to admit of a certain amount of variation in this respect, all will realise that such a difference would shake the reliability of venation too much.

I think that the latter explanation must be the correct one. As far as I am aware, Sir George Hampson had no wing-preparation made of such critical specimens, but at most made the wing somewhat transparent with a drop of toluol. Where he had only one specimen he would naturally not make a wing-preparation and perhaps not even use toluol, but satisfy himself by looking at the underside with a hand lens. After finding with toluol a difference between my specimen and the description, I sacrificed part of my specimen and mounted two wings in canada-balsam, thus making sure that my first observation was correct.

The genitalia in this genus (Pl. XXXI, fig. 11) present no special features, but are typical of the EPIPASCHIINAE.

Only one species so far recorded.

Genus **Apocera.**

Apocera, Schaus, 1912, Ann. Mag. Nat. Hist., (8) **9** : 660.
Holland & Schaus, 1925, Ann. Carnegie Mus., **16** : 55.

Type : *costata*, Schaus.

No specimen in my collection.

Genus **Lepidogma.**

Lepidogma, Meyr., 1890, Trans. Ent. Soc. Lond., **1890** : 472.
Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 459.

Type : *tamaricalis*, Mann.

Unfortunately I have not been able to study the type of this genus and have made the figures and observations from *L. rubricalis*, Hmpsn.

Pl. XXVII, fig. 10; Pl. XXVIII, fig. 13; Pl. XXX, fig. 9; Pl. XXXI, fig. 12.

The venation of *rubricalis* agrees with the description given by Hampson and would come in section IA, in which this worker also placed *tamaricalis*, except that the approximation of vein 4, 5 in both wings is hardly distinct, particularly in the hind-wing; * veins 6, 7 of hind-wing are from a point, not stalked. I am not sure that the maxillary palpi are three-jointed, for at the most only a faint transverse line can be seen. The angle at which the last joint is set in relation to the previous joint is very typical for this genus. The process of the antennae is long and slender.

The genitalia are typical of the subfamily, except that the juxta has a number of short thorns and the valves have near the base at one-fourth a tooth-like projection, a little over half the width of the valve.

Unfortunately only *rubricalis* is represented in my collection and then by males only, so I have to leave the study of other species, placed here, to the future.

Genus **Jocara.**

Jocara, Wlk., 1863, List Lep. Ins. B.M., **27** : 115.
Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 460.
Holland & Schaus, 1925, Ann. Carnegie Mus., **16** : 86.
Cacozelia, Grote, 1877, Proc. Boston Soc. Nat. Hist., **19** : 263.

Type : *fragilis*, Wlk.

Description and figures from *J.* (*Toripalpus*) *trabalis*, Grote.

Pl. XXVII, fig. 11; Pl. XXVIII, fig. 14; Pl. XXX, fig. 10; Pl. XXXI, fig. 13.

Unfortunately the genotype is not known to me, but *trabalis* appears to be very close to it, except that the hind-wing has veins 4, 5 and 6, 7 very shortly stalked.

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* Yet on this character is mainly based by Hampson in his key the difference between *Lepidogma* and *Jocara*, although the hollow labial palpi and the brush-like maxillary palpi are much more important characters.

Antennae with a very short pointed process, provided with a very long tuft of hair; shaft fasciculate with the cilia a little over two times shaft. Labial palpi with second joint six times first joint, hollow to receive brush; third joint acuminate and as long as first joint. Maxillary palpi are very peculiar in this genus in the way the third joint is set to the second joint; two last joints provided with long brush-like hairs. Hind tibia with two pairs of spurs.

About the genitalia there is nothing very remarkable. The uncus is rather broad and covered with rather long hairs at tip; valve sole-shaped, usually with a fold or projection near base and tipped with long hairs, which point inwardly.

J. argentilinea and *J. rufiapicalis* I remove from here to *Milgithea*, a genus closely allied to *Jocara*, I think, but peculiar for the jointed antennal processes.

Cacozelia basiochrealis, Grote, I place here and thus sink the name as a synonym of *Jocara* rather than of *Stericta*, as Hampson has done. On what grounds this was done I do not quite follow, for vein 8 of hind-wing is certainly not free, but anastomoses with 7. Venation, as well as palpi, antennal processes and genitalia agree in every respect with *Jocara.*

The following species have been studied and show the compactness of this group :—

Jocara sara, Schaus, Pl. XXVIII, fig. 18; Pl. XXX, fig. 12.

The fore-wing has vein 10 shortly stalked with the stalk of 7, 8, 9, and vein 6 is more remote from the stalk; veins 4, 5 of hind-wing are remote and not stalked. The hollow part of the second joint of the labial palpi is closed up at base; the third joint is shorter and the maxillary palpi have joint 2 and 3 of another shape. The antennal process is much longer. The genitalia have the uncus shorter, scaphium more sinuate towards tip, the juxta has a number of thorns and the valve is somewhat more curved.

Jocara ferrifusalis, Hmpsn., Pl. XXVIII, fig. 16.

The fore-wing has vein 6 rather remote from the stalk of 7, 8, 9; hind-wing with vein 4, 5 from a point; labial palpi with second joint somewhat closed, third joint very small; maxillary palpi with second and third joint almost parallel; antennal process even longer than in *sara* and more curved; genitalia as in *trabalis* but scaphium a little more curved in the middle.

Jocara (*Deuterollyta*) *conspicualis*, Led., 1863, Wien. Ent. Monats., **7 :** 359, Pl. 7, figs. 16, 17.

(*Stericta*) Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896 :** 472. Pl. XXXVII, figs. 7, 8.

The specimen I have thus identified at the B.M. does not quite agree with Lederer's figure, but the markings agree except that the hind-wing has in my specimen less outer marginal border.

Why Hampson placed this species in *Stericta* and not in *Jocara* (if it had to be sunk as a synonym) I cannot understand, for vein 8 of hind-wing certainly anastomoses with 7 for some distance.

I do not know whether Lederer's genus is worth preserving, for the only peculiarity that I can find lies in the base of the abdomen, which has a hair-pencil such as I have not found so far in any other member of this subfamily. For the time being it is, however, best placed in *Jocara.*

Jocara albimedialis, Pl. XXVII, fig. 6*e*; Pl. XXVIII, fig. 6; Pl. XXX, fig. 8; Pl. XXXI, fig. 5.

(*Pococera*) Hmpsn.
= *P. melanoleuca*, Druce (*nec* Hmpsn.) *Teste* Hmpsn.

As explained before, this species is better placed here.

Genus **Oedomia.**

Oedomia Dogn., 1906, Ann. Soc. ent. Belg., **50** : 120.

Type : *hispida*, Dogn.

Pl. XXVII, figs. 12, 12*a*; Pl. XXVIII, fig. 17; Pl. XXX, fig. 13.

This genus was formed by Dognin on one male specimen only, which, owing to lack of material and the peculiar structure of the fore-wing, was insufficiently examined, as the author acknowledges in the description. It is one of the many regrettable instances of new genera being formed on insufficient material. But it is still more regrettable that Hampson for similar reasons promptly places this species in his ms. notes in *Jocara* as a special section of that genus characterised by :—" antennae of male with the process long and thickly scaled; fore-wing with the apical part of costa dilated into a large rounded lobe with fringes of scales, recurved from it over upper surface and some rough scales below the fringe." In this group he also placed *J. oediperalis*, Hmpsn., and *J. albiferalis*, Hmpsn.

The two first species are unknown to me from specimens, but of *J. oediperalis* a male was known to Hampson, and the characters given above and mentioned by him in the description of this species indicate an affinity with *hispida*. The same holds for *albiferalis*, of which also a male is described.

Whether the venation for these two species is as Hampson gives for *Jocara* I doubt, as probably the lobe of the fore-wing in this case also prevented a proper study of the costal veins unless a preparation was made. The reasons why Hampson did not accept *Oedomia* as a good genus are, I think, firstly because it is based on male characters, secondly because the venation was not sufficiently studied. If we had to reject genera for the first reason many more genera would have to fall out, for instance the genus *Araeopaschia*, based on *rufescentalis*, of which also only males were known. (Hmpsn., 1906, Ann. Mag. Nat. Hist., (7), **17** : 134.) If genera are formed on the stalking of veins 4, 5 or the anastomosing of 7, 8 in hind-wing then surely there is ample reason for doing so when a vein is absent, as is the case here, where veins 9, 10 are coincident.

The figures make further description unnecessary, but I would like to add, that the hind tibiae have median spurs, the inner spur being over twice as long as the outer spur. Only males are known to me.

Genus **Titanoceros.**

Titanoceros, Meyr., 1884, Trans. Ent. Soc. Lond., **1884** : 62.
Hmpsn. (as syn. of *Jocara*), 1896, Trans. Ent. Soc. Lond., **1896** : 460.

Type : *cataxantha*, Meyr.

Pl. XXXVII, fig. 5.

I have two specimens in my collection from Brisbane, undoubtedly correctly identified, for, as Meyrick states, this species is easily recognised by its yellow hind-wing. I fail to see why Hampson placed this species in *Jocara*, for the labial palpi are solid and not at all as in *Jocara*, while the maxillary palpi are three-jointed in the ordinary way and triangularly scaled. (The statement made by Meyrick about them *l.c.*, p. 62, is probably due to their small size, for without dissection they are not readily observed.)

My specimen has veins 4, 5 of hind-wing more remote than in the fore-wing, but it is possible that this character varies.

The genitalia are peculiar for the shape of the uncus and for the toothed processes at the base of the scaphium, a character so far not found in any other member of the EPIPASCHIINAE. I think this genus can be kept distinct and placed somewhere near *Jocara*.

Genus **Milgithea.**

Milgithea, Schaus, 1922, Proc. Ent. Soc. Wash., **24** : 208.
,, Holland & Schaus, 1925, Ann. Carnegie Mus., **6** : 53.

Type : *melanoleuca*, Hmpsn.

Pl. XXIX, fig. 14; Pl. XXX, fig. 35; Pl. XXXVI, figs. 4, 5.

This I certainly consider a good genus, though also very near to *Jocara*. The most peculiar character is the jointed antennal process, which Dr. Schaus described as "bent back and with its end downturned." The dense hairs and scales make this jointing difficult to observe. Further, the hind tibiae have terminal spurs only; apparently in *Jocara* and *Oedomia* there are two pairs. The palpi show affinity to *Jocara*, especially the maxillary palpi.

Description and figures from *M.* (*Pococera*) *melanoleuca*, Hmpsn.

Fore-wing with the venation almost as given by Schaus, but my specimen shows vein 10 quite free, though very close to stalk of 7, 8, 9, so close, that in a not denuded wing it may appear as if they anastomose; vein 7 comes from 8 *beyond* 9, and this separates the genus from *Pococera*. Hind-wing as given by Schaus.

The genitalia show close relationship to *Jocara* and have no special peculiarities.

I also place the following species here, which were placed elsewhere by Hampson and Schaus.

Milgithea (*Macalla*) *argentilinea*, Druce.

Pl. XXX, figs. 15, 15*a*; Pl. XXVIII, fig. 15.

Venation of fore-wing is as in *melanoleuca* except that 4, 5 are not stalked but approximated; 6 is shortly stalked with stalk of 7, 8, 9; vein 7 is from stalk of 8, 9; hind-wing is the same as in the previous species.

The antennal process has here two projecting teeth on the basal joint, while the previous species has no tooth and the following only one. The labial palpus has the second joint rather long and the two last joints of the maxillary palpus have a different position from that of the maxillary palpus in the previous species, but probably the joints can move a great deal.

In the genitalia the structure is the same, only the valve is here less broad at middle and the apex is more rounded off.

Milgithea (*Jocara*) *rufiapicalis*, Hmpsn.

Pl. XXVIII, fig. 19; Pl. XXX, figs. 14, 14*a*.

The type specimen was a male, according to the description, and not a female as given by Schaus; evidently this species was not known to Dr. Schaus from specimens.

Fore-wing with the venation as in *melanoleuca* except that vein 7 comes from the stalk of 8, 9; in the hind-wing veins 4, 5 are on a very short stalk; labial palpi as in *melanoleuca*, but with the second joint a little more curved; maxillary palpi as in *argentilinea*; process of antennae with one tooth on outer side of basal joint; genitalia as in *melanoleuca* but valve narrower and of even width, apex very much rounded.

The three species studied form a very homogeneous group though, judging by outward appearance only, one would not suspect this. They are a good example of the necessity for detailed study of structure.

Genus **Astrapometis.**

Astrapometis, Meyr., 1884, Trans. Ent. Soc. Lond., **1884** : 67.
,, Hmpsn., 1896, Trans. Ent. Soc. London., **1896** : 461.

Type : *saburalis*, Wlk.

A male specimen kindly presented and identified by Mr. E. Meyrick has been studied by me and very little is to be added to the original description. The affinity is not quite clear to me; the labial palpi are practically as in *Cecidipta excaecariae* (Pl. XXVIII, fig. 24), and the maxillary palpi are almost so, but the scales and hairs are shorter; the venation is practically as in that species, except that vein 8 of hind-wing anastomoses with 7, while in *C. excaecariae* it is free. It is still to be proved, however, that this character is of sufficient importance to use it for the grouping of genera, as is done by Hampson. The process of the antennae is as in *Tancoa metaxanthalis* (Pl. XXX, fig. 4), with which it has nothing further in common; the hind tibiae have four spurs each.

The genitalia are like those of *Jocara* or *Milgithea* except that the uncus is rather broad, at least as in *M. argentilinea*, and there is an indication of coremata at the base of the valves. The valves are as in *M. argentilinea* but broader at base and a little more pointed, almost the shape of a parallelogram. Two species have been placed in this genus, *saburalis*, Wlk., and *elasota*, Meyr. The latter species is unknown to me and was placed by Meyrick in *Epipaschia* and by Hampson in this genus, according to his ms. notes and the arrangement in the B.M. The genus belongs to the Australian fauna.

Genus **Termioptycha.**

Termioptycha, Meyr., 1889, Trans. Ent. Soc. Lond., **1889** : 504.
,, Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 462.

Type : *cyanopa*, Meyr.

Pl. XXVII, fig. 13; Pl. XXVIII, fig. 23; Pl. XXX, fig. 16; Pl. XXXI, fig. 14.

The descriptions given by Meyrick and Hampson agree on the whole with my specimens, but the fore-wing has vein 4, 5 as a rule remote, and vein 3 of hind-wing does not approximate to 4, 5. The maxillary palpi are not filiform, but the scales are somewhat spreading, so as to make it triangular. In some specimens the hind-wing shows also an outer marginal fold which, however, is never as broad as in the fore-wing. The broad fold on the fore-wing is a very peculiar feature and has never been found by me on the outer margin in any other species; it probably covers androconia. A similar fold is also found on the costa of the hind-wing.

The genitalia are very peculiar in this genus and differ from those of most EPIPASCHIINAE in the weak but peculiar development of the scaphium, which is very short, probably not jointed, and provided with many thorns or stiff bristles. The uncus is broad and somewhat bifid; the valve has one thorn on the apex and the vesica is provided with four thorns, one of which is very stout; the vinculum is very broad at base, forming a saccus. There is no doubt about it in my mind that this genus occupies a rather isolated position.

I place also in the genus the following species :—

Termioptycha (*Parasarama*) *conjuncta*, Warr., **117 :** 454, Ann. Mag. Nat. Hist., (6) 896.

Pl. XXVIII, fig. 21; Pl. XXX, fig. 17; Pl. XXXI, fig. 16.

This species was sunk by Hampson as a synonym of *M. margarita*, Butl., but later on in his ms. work and in the B.M. collection it was re-established. I have this species from New Guinea and one specimen from Ceylon. It is certainly distinct from *margarita*, Butl., though, superficially, it resembles that species somewhat. It is not surprising that Hampson placed it in his omnibus genus *Macalla*, but from the structure it will be seen that it is better placed here.

The venation differs only in one important respect, namely the independent origin of vein 10 in the fore-wing, though it closely approximates the stalk of 7, 8, 9, so much so that it would not be noticed in a specimen from which the scales are not removed. However, it is this character that makes, according to the description, a great difference between *Termioptycha* and the following genera.

The absence of the terminal fold of the fore-wing naturally eliminates the peculiar curving of several veins in that region, as found in *cyanopa*. The basal joint of the antennae is as in *cyanopa*, but the labial palpus is somewhat modified as the first joint is much more curved at two-thirds, while the terminal joint is much shorter.

The genitalia show much resemblance. The uncus, though shorter and broader, is bifid; the scaphium is reduced to two disconnected blunt processes, densely covered with stout hairs; the shape of the valve is slightly different, but it also has a stout thorn on the apex; the vesica has three, but very strong and curved thorns; at base of the juxta there are two slender processes, not found in *cyanopa*; the vinculum is more stout and broader and not produced into a saccus.

Termioptycha aurantiaca, sp. n.

Pl. XXXI, fig. 15.

Venation as in *T. conjuncta ;* the hind-wing has, however, a well-pronounced rounded anal lobe; basal joint of antennae as in Pl. XXX, fig. 17; shaft biciliate; labial palpi precisely the same as in *cyanopa* (Pl. XXVIII, fig. 23); maxillary palpi as in Pl. XXVIII, fig. 23, but second joint a little larger and the third joint somewhat smaller, tuft of scales a little longer; genitalia as in *cyanopa* but scaphium more fully developed; valves as in *cyanopa* except that the basal triangular process is more developed than in *cyanopa*; the thorn at apex is stouter; at base of valves there is a stout rounded process; aedoeagus very long and pointed; vesica provided with a series of thorns; vinculum broad as in the other two species but produced into an even longer saccus than in *cyanopa*.

Male. Head, palpi, thorax, abdomen, legs, fore-wing above and both wings on underside buff-yellow (iv); hind-wing above ochraceous-buff (xv), irrorated with fuscous (xlvi); fore-wing with a basal dense fuscous irroration from upper median to inner margin, parallel with antemedial line and leaving a light curved fascia between; a curved fuscous antemedial line, indistinct from costa to lower median, then well defined to inner margin; a triangular fuscous mark from middle of costa into end of cell; a small fuscous irroration beyond discocellulars, mixed with white tufts of scales; a fuscous postmedial line from two-thirds of costa to near termen at vein 3, then angled inwardly to base of vein 2, then zigzagged at 1*a* to two-thirds of inner margin; less dense fuscous irroration between the angled postmedial line and lower inner marginal area; apical area beyond postmedial line irrorated with clay colour (xxix), leaving a narrow line of ground-colour beyond postmedial line. Hind-wing with a fuscous apical irroration preceded by a narrow postmedial irroration from costa to 1*c*, forming two darker maculae between 1*c* and 2; a patch of shiny scales along costa, covered by inner margin of fore-wing.

Underside: Fore-wing with some fuscous irroration on medial area before costa; a patch of shiny androconia along inner margin; on hind-wing a pocket formed by a fold in the wing between 1*b* and 1*c*, filled with very long scales.

Exp. 30 mm.

Hab. New Guinea.

Type: Arfak mountains, 4000 ft., Febr.–March 1909; cotypes: Mt. Kunupi, 6000 ft., Nov.–Dec. 1920; Mt. Kebea, 3000 ft., July 1903; all collected by A. E., C. B., C. F. and J. Pratt.

Genus **Omphalota.**

Omphalota, Hmpsn., 1899, J. Bombay Nat. Hist. Soc., **12**: 479.

Type: *chlorobasis*, Hmpsn.

No specimen in my collection.

So far only one species has been described in this genus, from Simla.

Judging from the description this genus and the following are closely allied to *Termioptycha*, from which they differ in having the fore-wing with vein 10 free, a character that may, however, also be found in that genus in which case there would be then a close approximation of the venation.

Genus **Araeopaschia.**

Araeopaschia, Hmpsn., 1906, Ann. Mag. Nat. Hist., (7) **18**: 134.

Type: *rufescentalis*, Hmpsn.

I have no specimens belonging to this genus in my collection. In ms. notes and in the B.M. collection Hampson also places *Stericta demotis*, Meyr., in this genus.

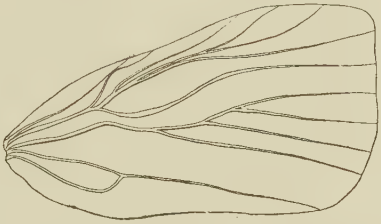
The difference between *Araeopaschia* and *Omphalota*, as given in a ms. note by Hampson, is only in the cell of the fore-wing being short in *Omphalota* and long in *Araeopaschia*. Comparing the descriptions of the two genera, no other important characters can be relied on.

Genus **Spectratrota.**

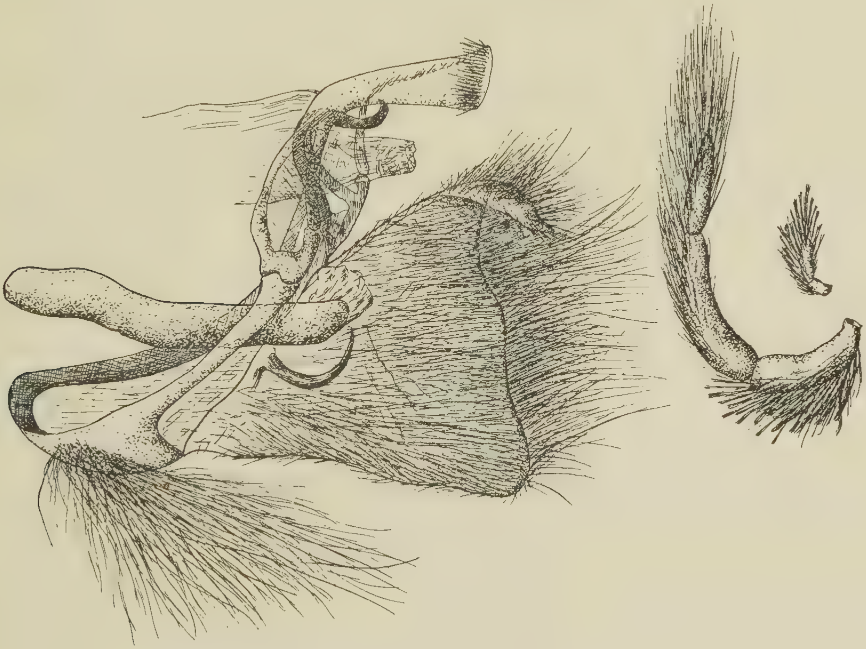
Spectratrota, Warr., 1891, Ann. Mag. Nat. Hist., (6) 7 : 426.
,, Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 462.

Type : *fimbrialis,* Warr.

The description given by Hampson is on the whole correct (though the figure does not show the correct course of the veins), except that the fore-wing has vein 10 not free but stalked with 7, 8, 9. In the preparation I made the air in the stalk of these four veins was still present, showing clearly that it is one very thick stalk which forms the upper part of the fovea, while vein 6 is much curved downwards to form the lower margin of it. However, such details can hardly be made out unless the wing is denuded. Vein 11 is very much curved upwards so as almost to touch vein 12, which is very weak and short. The discocellulars are invisible, even in the preparation; in the hind-wing these are very oblique.



Text-fig. 1.—Fore-wing of *Spectratrota fimbrialis*, Warr. ♂. × 8. Janse del.



Text-fig. 2.—Genitalia (× 38) and palpi (× 26) of *Spectratrota fimbrialis*, Warr. ♂. Janse del.

The genitalia are rather peculiar in the genotype; the triangular shape of the valves, with the curved-up anal angle I have not found in any other EPIPASCHIINAE that I have studied; each valve also has a long upwardly curved hook at base.

The antennae are without a process in the male, and the hind tibiae have each two pairs of spurs of which the inner spur is three times as long as the outer spur.

Hampson in his ms. notes places also three other species here: *normalis*, Hmpsn., also from Australia, *erythrolepia*, Hmpsn., and *catena*, Wileman, both from Formosa. Of the latter only a female is known. None of these three species is known to me.

Genus **Geropaschia.**

Geropaschia, Hmpsn., 1917, Ann. Mag. Nat. Hist., (8) **19** : 361.
Araeopaschia, Hmpsn., 1916, Ann. Mag. Nat. Hist., (8) **18** : 134, *nec* Hmpsn. (1906).

Type: *Araeopaschia grisealis*, Hmpsn.

In 1916 Hampson proposed the new genus *Araeopaschia* for *grisealis*, overlooking the fact that this name was already used by him in 1906 (Ann. Mag. Nat. Hist., (7), **17** : 134); this he rectified by proposing the name *Geropaschia* for *grisealis* in 1917.

No specimens are known to me.

Genus **Macalla.**

Macalla, Wlk., 1858, List Lep. Ins. B.M., **16** : 155.
,, Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 463.

Type: *thyrsisalis*, Wlk.

In this genus a large number of genera were placed by Hampson as synonyms, but a glance at the species placed in this one group shows at once that we here have to deal with an omnibus genus, produced, no doubt, by excluding secondary male characters in defining the genera.

A close study of the structural characters, however, reveals quite a number of groups of the rank of a genus; a number which, when more material is studied, will increase and not decrease.

Study of the venation only is here extremely misleading, but that of the palpi and genitalia has proved most helpful in arriving at a more natural classification.

A description of the genotype will now be given, and for specimens and information on this species I am very much indebted to Dr. W. Schaus and Mr. W. H. T. Tams, the former for sending me a male, the latter for making structural drawings from the male type. Mr. Tams' drawings coincide entirely with the preparation made by me from the specimen I received from Dr. Schaus, so I have not the slightest doubt about the correctness of the identification, though errors are easily made in this group.

Macalla thyrsisalis, Wlk.

Pl. XXIX, fig. 1; Pl. XXXVII, figs. 12, 13, 14, and text-figure.

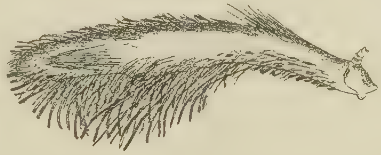
Male. There is no important difference in the venation of the two sexes and the venation agrees quite well with Hampson's figure and description, except that the fore-wing has vein 6 shortly stalked and the hind-wing has vein 3 from well before angle.

Labial palpi upturned, well above vertex of head, most of its length is taken up by the second joint, which is hollow to receive the brush of the maxillary palpi; second joint thickest at two-thirds, covered on inner and outer side with scales and hairs mixed; third joint minute. Maxillary palpi three-jointed, second and third joints angled to the first and close together, as if they come from end of first joint; these two last joints with long hairs, which form a brush to fit into labial palpus.

Hind tibia with two pairs of spurs, outer spur smaller.

Genitalia: Uncus simple, rounded, broad at base; scaphium normal; valves sole-shaped, rather narrow towards apex and with a long, sinuous, pointed process at base; juxta with two long, thin, curved processes; aedoeagus stout, broad at tip and there provided with a single row of long spines, which are directed inwardly, vesica smooth; vinculum forming a long saccus.

Besides *thyrsisalis*, Hampson also places in this section of *Macalla* the following species :—*regalis*, *sinualis*, *noctuipalpis*, *euryglauca*, all from America; *hypoxantha*, *minoralis*, both from India; *melapastalis*, *purpureopicta* and *olivaris*, all from Africa. Of the African species only *melapastalis* has been studied by me (Pl. XXXIII, fig. 6), in which the venation, palpi and antennal process agree very well, yet the genitalia are rather different. The uncus is somewhat reduced and probably not lobed; the penis has a chitinised narrow pointed rod, almost as long as the valves; the valves are more blunt and the terminal margin is more erect, broad and with rounded angles, while no basal process is present. However, I see no reason for keeping it out of this genus.



TEXT-FIG. 3.—Antennal process of *Macalla thyrsisalis*, Wlk. × 8.

The Indian species mentioned above are unknown to me, but I have a strong suspicion that the true *Macalla* is confined to America. Even Indian species, such as *amica*, which resemble *thyrsisalis* mostly in general appearance, differ far too much to keep them in this genus. However, further study will have to decide this, as material becomes available.

The following genera, formerly sunk under *Macalla*, I remove therefrom and treat them as valid.

Genus **Lamida.**

Lamida, Wlk., 1858, List. Lep. Ins. B.M., **16** : 252.

Type : *moncusalis*, Wlk.

Hampson makes this a section of *Macalla* with the following characters :—" male with second joint of palpi short, third immensely dilated and curved over vertex of head, with a hollow containing the maxillary palpi, which are tufted with long hairs; paired tufts of hair behind the antennae."

As will be seen in my figure, it is not the *third* but the *second* joint that is thus dilated, and therefore the whole section can be merged into Hampson's Section II. For other reasons, however, I think this species forms, together with some other species, a compact group of generic rank.

Description from male of *moncusalis*, Wlk.

Pl. XXX, fig. 19; Pl. XXXV, fig. 3; Pl. XXXII, fig. 9.

Antenna with the basal joint bearing a blunt, short projection covered with scales. Labial palpi upturned, much curved; second joint more than twice length of first joint, thickened and hollowed out at terminal half and with rounded scales inside the cavity and long yellow-brown hairs on the outer edge; third joint small, thin and curved, almost hidden in hairs and scales. Maxillary palpi three-jointed; first joint thin, second thick and elbowed to first joint, third long and thin; these two last joints with long blackish-brown hairs, which can just reach the hollow of the labial palpi.

Genitalia: Uncus bifid; scaphium absent (reduced, as one of the included species clearly shows); juxta with two curved processes at base; penis simple; valves sickle-shaped, with a small tooth just before middle on lower margin.

In some species (*moncusalis* and *mediobarbalis*) there is a tuft of scales and hairs mixed on upperside of fore-wing from upper median towards end of cell. In the two other species this tuft seems to be lost.

I place the following species in this genus :—

Lamida mediobarbalis, Hmpsn., 1916, Ann. Mag. Nat. Hist., (8), **18** : 135.

Pl. XXXV, fig. 4; Pl. XXXII, fig. 13.

Male. Antennae without process; labial palpi as in *moncusalis*, but with the hollow part as large as two-thirds of second joint, hairs very long, yellow and coming mainly from the base and not from along the edge; third joint absent (the little projection on the second joint is homologous with the larger projection in *moncusalis* and is not the third joint, as two preparations clearly showed under high magnification). Maxillary palpi absent. (Two separate specimens were dissected to make sure of this and one labial palpus was opened up at base in case the maxillary palpus was hidden there, but not a trace of it could be found.) This is certainly interesting as it shows a tendency to reduce one organ if the function is taken over by another. The rounded scales in the hollow are very thick and fluffy, and I have no doubt that they are of a glandular nature.

Genitalia: Uncus bifid, lobes rounded and curved; scaphium absent; juxta with two long processes of unequal shape and size, left process long, pointed and sharply curved; right process half that length, straight and rounded at the end; valves pear-shaped, terminal rounded part densely covered with long, inwardly directed hairs; a small rounded projection near outer margin just before the hairy part on inner side of valve; vinculum better developed than in *moncusalis*, but narrow at lower part; penis with long stout spine below at tip.

This species is recorded from Sikkim and Borneo; my specimens come from Buru and New Guinea.

Perhaps this species is the most reduced of those that I here include in the genus.

Lamida sordidalis, Hmpsn., 1916, Ann. Mag. Nat. Hist., (8), **18** : 136.

This species was placed by Hampson in the *Lamida* group, but he makes no special mention of the palpi in the description. The male, from which my preparations are made, agrees in every respect with the females I have, one of which I have compared with Hampson's type.

Pl. XXXV, fig. 8; Pl. XXXII, fig. 11.

Male. Antennae without a process; labial palpi upturned, recurved over frons, second joint about three times first joint, hollow for over two-thirds of its upper length; a thick brush of broad, flat, light brown hairs from base of hollow; these hairs have fine punctuations, which indicates that they are probably glandular; third joint thin, curved. Maxillary palpi three-jointed, filiform, triangularly covered with hair. The maxillary palpi are too small even to come in contact with the glandular hairs and will not reach as far as hollows of labial palpi.

Genitalia: Uncus deeply bifid; scaphium absent; juxta with two long processes, curved at tip and surrounding the aedoeagus; valve sickle-shaped and with small curved hook from outer margin before middle; vinculum long and of even width, fairly broad; penis short, stout and without armature.

Lamida perdentalis, Kenr.

My male, from which the observations are made, is somewhat darker than the female (kindly presented to me by Sir George Kenrick), which has more white scaling on the hind-wing, but I have no doubt that it is identical.

Pl. XXXV, fig. 5; Pl. XXXII, fig. 10.

Antennae without process at base, shaft ciliated. Labial palpi upturned, second joint solid and a little over twice first joint, third joint a little shorter than first; long downwardly directed hairs in front of second and third joints, first joint triangularly covered with hair, third joint with a series of downwardly directed stiff bristles and a curved brush of hairs terminally; maxillary palpi filiform, covered with hairs, first joint angled at tip, second cylindrical, third short and roundly pointed.

Genitalia: Uncus bifid, lobes short, broadened towards the end; scaphium absent; juxta with a curved shield anteriorly and two long, stout, curved processes posteriorly; vinculum rather narrow; valves short, broad, apex curved upwards; one long narrow process from base at one-third, apically covered with hairs; a broad triangular process near base at lower margin; valves covered on inner side with long hairs directed anteriorly.

Lamida buruensis, sp. n.

Male. Palpi, head, thorax and ground-colour of fore-wing olive-ochre (xxx); fore-wing with a narrow, very oblique antemedial line from costa a little beyond base to 1*b* before middle, where it is sharply angled inwardly; a fuscous diffuse macula at costa before middle; a brush of moderate fuscous-black hair beyond it in cell; postmedial line diffuse, fuscous-black, from two-thirds of costa to vein 5 at two-thirds, then angled inwardly and obsolete to vein 2, sharply angled at 2 and 1*b* and then to inner margin at two-thirds, where it is more diffuse; a fuscous suffusion beyond the postmedial from near apex to vein 6 and from vein 3 to 1*b*, leaving a lighter terminal patch interrupting it; a fuscous terminal series of elongate spots between the veins; cilia evenly suffused with fuscous.

Hind-wing semi-transparent, heavily suffused with fuscous, especially towards apex and along outer margin; cilia suffused with fuscous; a patch of iridescent scales along apex costal area.

Underside: As on upperside, but markings less pronounced, ground-colour and suffusion of both wings lighter and no brush of hair in cell of fore-wing.

The cotype male is much paler in ground-colour and more heavily suffused with fuscous, thus appearing generally much darker.

In general appearance this species is almost like *sordidalis*, with which it can be easily confused unless the palpi are studied; from *perdentalis* it may be more easily distinguished by the colour of the fore-wing, though the markings are very similar.

With regard to its generic position, this species seems to be best placed here, although the palpi are somewhat different from those of the three preceding species. Their structure, however, suggests that the second joint has still the solid form, though in general shape the whole palpus resembles that of *sordidalis* somewhat.

The genitalia, though peculiar, show at least two important characters found in this group, namely the bifid uncus and the absence of the scaphium.

Antennae without the process; labial palpi upturned, reaching a little above vertex of head, second joint twice first joint, solid, thin in middle and broad at tip, where it becomes bifid (here I suspect some of the hairs and scales to be glandular); third joint small and pear-shaped; palpus in front covered with scales mixed with hairs, on the inside covered with long hairs. Maxillary palpi three-jointed, second joint elbowed to first joint; joints of same length, somewhat pear-shaped; second and third joint covered with long hair.

Genitalia: A few stout hairs from top of eleventh tergite to cover part of the uncus; uncus bifid, lobes broad, sickle-shaped and tipped with long hairs; scaphium absent but two short curved processes are found on the eleventh tergite indicating the remains of it; juxta with one long stout spine in middle, almost as long as the penis; penis rather small and without armature; valves broadly sickle-shaped and with a long fold at base on lower margin; vinculum broad above, narrow below.

Hab. Type male and cotype male, W. C. Buru, Miapat, 5000 ft., April 1922, Pratt.

Exp. Type ♂, 30 mm.; cotype ♂, 29 mm.

Genus **Teliphasa.**

Teliphasa, Moore, Lep. Atk., p. 200 (1888).
Hmpsn. (as syn. of *Macalla*), 1896, Trans. Ent. Soc. Lond., **1896**: 463.

Type: *nubilosa*, Moore.

I have in my collection a specimen from the Atkinson collection from Darjeeling with a small red label bearing the number 140 and above it a label with: "coll. Staudinger." Then follows a label giving in French the generic characters, which fit well on the whole, except that the maxillary palpi are supposed to be absent, which is not the case. Under this description is the name *Teliphasa*, and in the same handwriting follows a label with *Teliphasa nubilosa*, Moore, on it. This specimen I compared in the B.M. and found it identical with the type.

Whether this species is the same as *derogatella*, Wlk., I do not know, but Hampson certainly gives an incorrect description of *Teliphasa* in Section II of *Macalla*, as the maxillary palpi are not filiform and it is not joint three but the second joint of the labial palpi, which is further correctly described. I have no doubt that my other specimens of *nubilosa* are the same as the one mentioned above, and that therefore it will be correct to consider *Teliphasa* as a distinct genus.

The species *amica*, Butl., was placed by Hampson in the *Lamida* section, probably on account of the palpi, but many structures, partly found in other species, are so peculiar that I think them of generic importance. The loose scaphium, with the points hanging downwards, excludes it at once from the preceding groups, though the affinity with *Lamida* is quite clear.

The specimen of *amica*, from which the description and figures are made, is a Sumatran male and identical with my Japanese specimen except that I cannot see the hook on the aedoeagus in the latter, a character also absent in the Chinese specimen (Pl. XXXII, fig. 5), which also lacks the white scaling on the fore-wing.

Pl. XXVIII, fig. 22; Pl. XXXI, fig. 17; Pl. XXXII, fig. 5; Pl. XXXV, fig. 7.

Male. Antennae without projection, shaft fasciculate, hairs longer than thickness of shaft; first joint globular. Labial palpi upturned, reaching well above vertex, second joint four times first joint, hollow for terminal half, where it is club-shaped; in this hollow fits the brush *from the frons*, but the inside is not covered with scent scales; the outside and the front of the second joint densely covered with short broad scales; third joint small, globular. Maxillary palpi possibly two-jointed (in the two dissections only two joints were found), both joints semi-globular and triangularly scaled with broad scales. Here as well it is quite clear that the maxillary palpi have nothing to do with the hollow cavity of the labial palpi. A thick tuft of hairs from lower middle of frons, covered by the hollow of the second joint of the two palpi, which here meet together, holding the tuft as if in a box. Whether these hairs are glandular or merely act as distributors I have not been able to make out yet.

Venation as given for *M. thyrsisalis* except that in the hind-wing vein 8 is just touching vein 7. Hind tibia with two pairs of spurs, outer spur half the length of the inner one.

Genitalia: Uncus reduced to a narrow strip of chitin around the anus; scaphium consists of two fairly long projections from each side below anus, disconnected at tip and somewhat hanging downwards but curved upwards. (From this and other species I conclude that the scaphium, though developed from the tenth sternite, lost its chitinisation *in the middle*, just leaving the two projections.) Valves rather thin and densely covered on the inner side with long inwardly directed hairs; fine parallel striae on inner side of valves; each valve forms a conical saccus at base beside the penis; aedoeagus with one strong, downwardly curved spine at tip; vesica without armature.

The specimens from China and Japan do not show this spine, and, if the Japanese specimen did not agree so well in all other respects with the one described above, I would feel inclined to consider the Chinese specimen as another species. As it is, the spine may be there, but lost in the preparation, or the position may prevent its detection. For the time being I keep the three together.

According to genitalia and venation, several more species should come in this genus, but the palpi are in all these different in being more or less solid and in having no hairbrush at all. However, the genitalia are so peculiar in this group and show so much specialisation, that I do not doubt that they form a perfectly natural group of generic rank.

The first that I desire to place here is *M. picta* from the Australian region and placed by Hampson in his Section IVB, *a*, *a′*, or as a subsection of *Parasarama*. The type of Warren's *Parasarama* is *cuproviridalis*, of which I have only females and the description is insufficient to decide whether it is a good genus or not, but its main difference is in the process of the antennae being or not being developed and further in the appearance of the palpi. Though I consider these characters of great importance, yet I think they should be confirmed by the genitalia, which I think are less liable to become modified, seeing how stable they remain even within the species. So pending future investigation they are better kept here.

Teliphasa picta, Warr.

Pl. XXXII, figs. 1–4.

Male. Antennae without a basal process. Labial palpi upturned, almost as in Pl. XXVIII, fig. 3, but third joint in line with second joint; maxillary palpi as in Pl. XXVIII, fig. 3, but only two joints in my preparation (the first remained probably on the specimen, but I cannot see it). Hind leg with two pairs of spurs, outer half the length of inner one.

Genitalia in general appearance as in *amica*, but the uncus is still there, though very short, rounded off and simple; scaphium is represented by two curved processes with the apex curved outwards; valve as in *amica*, but without the saccus at base; penis much bigger than in *amica*, aedoeagus almost twice the length of the valve; penis without armature.

As is shown in the three illustrations the shape of the valve may vary a little. In figs. 3 and 4 it is less rounded, but, in a rather soft valve, as is the case here, it may have shrunk in the preparation. The vinculum also shows some variation as in fig. 4; it is very narrow at middle. All specimens came from New Guinea.

Teliphasa nubilosa, Moore.

Pl. XXX, fig. 18; Pl. XXXII, figs. 6, 7, 8; Pl. XXXV, fig. 2.

According to genitalia as well as to other details, I think this species is best placed in this genus, although the first joint of the antenna has a short process. This type of genitalia has not been found by me in any other genera of the EPIPASCHIINAE, so this departure in the antennae may be looked upon as a character not yet sufficiently developed, thus showing more ancestral origin in the previous species. The absence of the uncus and the armature of the penis, as well as the structure of the labial palpus, bring this species closest to *amica*. In general aspect too it resembles *amica* more than any other species.

Male. Antennae with basal joint globular and provided at end with a recurved or straight process, almost as long as the first joint or somewhat longer; shaft bi-ciliate. Labial palpi upturned, well above vertex of head, long, slender; second joint three times the length of first joint, acuminate and incurved towards the tip, a narrow slit on inner side over the terminal half; third joint minute; second joint covered all over with dense hairs pointing downwards. Maxillary palpi (in drawing probably upside down) minute, first and second joint large and elbowed; third joint small; two last joints with long hairs and scales mixed. Hind tibia with two pairs of spurs.

Genitalia: Uncus absent; scaphium represented by two semicircular processes, which point upwards. (In fig. 8 they are represented somewhat inwardly, but that I consider the correct position; in fig. 7 they are drawn outwardly, which I think is due to displacement in the mounting, as they are very loosely attached to the membranes of the sternite.) Valves almost circular, very membranous and often somewhat pleated, densely covered with long inwardly pointed hairs; vinculum stout, of even width; no saccus; penis rather short, stout and aedoeagus provided with a slightly curved stout spike.

Lacalma, gen. n.

Type: *porphyralis*, Kenr.

In addition to the type I also place here *argenteorubra*, *albirufalis*, *papuensis*.

This group differs from *Macalla thyrsisalis* among other characters in the venation, as the fore-wing has veins 7, 8, 9 from a point or almost so. Where this is nearly so, vein 7 comes from *before* 9, as the stalking in this group has evidently been carried out further than in *M. thyrsisalis* and the previous allied genera.

Description from *porphyralis.*

Pl. XXX, fig. 22; Pl. XXXII, fig. 15; Pl. XXXIII, fig. 8; Pl. XXXV, fig. 11.

Antennae lamellate and fasciculate; antennal process long, broader at base than towards tip, covered on inner side with long hairs and long broad scales, on upper side with dense short scales. Labial palpi with second joint hollow over the whole length, over twice first joint; third joint half of first joint (as in *papuensis*, Pl. XXXV, fig. 10); maxillary palpi with the third joint almost from base of second joint; third joint with long brush of hair, second joint with still longer hairs.

Genitalia: Very much like *Epipaschia superatalis* but provided, as a rule, with coremata at the base of each valve. Uncus well developed, somewhat curved, broader at tip and rounded off, at tip a number of hairs pointing anteriorly; scaphium normal; vinculum narrow; two coremata at base of vinculum and valves provided with long hairs; valves sole-shaped, simple, without armature and densely covered with medium long hairs; aedoeagus and vesica without armature; juxta simple, as a rule well-developed.

I have no doubt that this is a good genus and I place the following three species here as well, removing them from *Macalla.* They all have the same type of marking and all belong to the same fauna. In addition I have a number of undescribed species which have to come here, but further material is still required, as I do not like to describe from one specimen only. The genitalia of these four species agree in every essential respect, yet there seems to be a tendency to lose the coremata.

Lacalma papuensis, Warr.

Pl. XXXV, fig. 10.

Differs from the previous species in the maxillary palpi not having long hairs, but instead fairly long scales. The genitalia are almost the same but I am not sure whether the coremata are present here or not; the bases of the valves indicate that they were lost in the preparation. The juxta is somewhat more developed.

Lacalma argenteorubra, Hmpsn.

The labial palpi have a somewhat deeper groove, but the maxillary palpi are as in Pl. XXXV, fig. 11. Antennal process very much as in Pl. XXX, fig. 22, but somewhat broader and with more hairs and scales on the upperside. Fore-wing with vein 7 from a little before 9.

Genitalia typical, but here too I have not been able to see any coremata, though at the base of the valves there is a clear indication that they have been there.

Lacalma albirufalis, Hmpsn.

Antennal process as in genotype but broader at base and scales rather longer. Labial palpi as in Pl. XXXV, fig. 10, but the second joint rather longer and more curved at base; maxillary palpi as in genotype. Genitalia as in genotype, but valves narrower and longer; coremata present.

Epilepia, gen. n.

Type : *melanosparsalis*, Janse.

Pl. XXX, fig. 20; Pl. XXXIII, figs. 1, 2.

The venation is almost the same as in *Macalla,* except that veins 4 and 5 are less close together in fore-wing and hind-wing. The greatest difference is, however, in the labial palpi, which are solid in the male and almost as in Pl. XXXV, fig. 12, except that the second joint is a little shorter and thicker, just twice the first joint, and the third joint is a little shorter than the first joint and less pointed; maxillary palpi as in fig. 12; antennae with a long slender process (Pl. XXX, fig. 20); hind legs with two pairs of spurs, of which the outer spur is a little over half of inner one.

Genitalia typical for this genus and do not resemble those of any other species placed in *Macalla* by other workers, as far as I have studied them. Moreover, the same characteristics are found in the other African species and it makes me think that this genus may be peculiar to Africa unless an Indian species (Pl. XXXIII, fig. 3) has to be placed here also, as it has the peculiar hook on the aedoeagus in common. But in that species the fore-wing has vein 10 very remote from the stalk of 7, 8, 9. Uncus broad and short, rounded; scaphium normal; vinculum broad at lower part; valves sole-shaped and with a process at base of upper margin (in *melanobrunnea* this process is less developed but still visible); juxta divided into two stout slightly hooked processes; aedoeagus with a large, stout, pendulous, lancet-shaped process.

Epilepia melanosparsalis, Janse.

Syn. :—*Macalla confusa*, Janse.

Pl. XXXIII, fig. 1; Pl. XXX, fig. 20.

Though these two forms look externally rather different in markings I have now, on comparing the genitalia, no doubt that they are the same species.

Epilepia melanobrunnea, Janse.

Pl. XXXIII, fig. 2.

Palpi and antennal process as given for the genus except that the process lacks the downwardly curved hairs at the tip. In the genitalia the process at the base of the valves is covered with short spines (not found in the two previous species); process on aedoeagus with spines on the posterior side.

Epilepia simulata, sp. n.

Pl. XXXVII, fig. 10.

Male. Very similar to *melanosparsalis* in markings and colour, but the basal patch on the fore-wing is smaller and more erect and slightly hollowed out instead of bulging towards median part of wing; a very faint line just beyond it; terminal half of wing also clear, but with a chamois (xxx) tinge; a number of black scales at end of cell and a small black macula just above it on costa; beyond costal macula is another black macula from which begins the postmedial line, which is curved inwardly below vein 2 and dentate on the veins; apical part filled in with black to vein 6, where it almost joins the postmedial line; a series of well-defined terminal spots between the veins; cilia chamois with black scales mixed.

Hind-wing in colour like light patch on fore-wing, but suffused with fuscous, especially on vein 2; termen suffused with fuscous-black, darkest at vein 2; cilia as in fore-wing.

Underside: Ground-colour light buff (xv) but irrorated with fuscous especially along margins; postmedial indicated by diffuse fuscous lines; a fuscous macula in cell of forewing.

The structure is as in *melanosparsalis* except that the labial palpi are a little shorter and thinner; the process of the antennae has the same characteristic hair and scale covering (see Pl. XXX, fig. 20), but the genitalia show some peculiarities not found in the others. Uncus, scaphium and valves are the same except that the latter have a somewhat smaller process; the aedoeagus has not the characteristic hooked process at tip, but instead a series of three stiff spiky bristles from the middle. There is also a peculiar chitinised circular band, with the ends overlapping a little, just behind the saccus. This ring I also found in the other specimen (cotype), so I am sure that it has some significance.

Exp. 21 mm.

Hab. Male type, Agbaja (N. Nigeria), Aug.–Sept. 1913 (*D. Cator*); male cotype, N'Dalla Tando (N. Angola), 2700 ft., 15 Nov. 1908 (*Dr. W. J. Ansorge*).

Calomacalla, gen. n.

Type: *Macalla metachryseis*, Hmpsn.

Pl. XXXIII, fig. 4.

The venations of both wings show affinity to *Macalla*, but in the fore-wing vein 10 is stalked with 7, 8, 9 for nearly half the length of the stalk, diverging from 9 more rapidly than in *thyrsisalis*. Antennae without process; shaft bi-fasciculate; labial palpi as in Pl. XXVIII, fig. 12, only a little stouter; maxillary palpi as in Pl. XXVIII, fig. 4, but last joint a little longer and more rounded towards the tip.

Genitalia unlike any of the *Macalla* group in the structure of the IXth sternite and the thorn on the vesica. Uncus rather short, broad and rounded off at tip. IXth sternite mainly made up of two upper and lower processes that are strongly chitinised and point towards one another, remainder membranous; on lower processes the normal and rather stout scaphium is fixed; vinculum very much as in *Epilepia*; valves rhomboid, roundly pointed and sparsely covered with hairs; juxta membranous; aedoeagus without armature; vesica covered with a large number of small, inwardly directed spines and with a large stout spine directed outwardly.

Only one species so far known to me, viz. *Calomacalla metachryseis*, Hmpsn.

Genus **Epipaschia.**

Epipaschia, Clem., 1860, Proc. Acad. Nat. Sci. Phil., **1860** : 14.
Hmpsn. (as syn. of *Macalla*), 1896, Trans. Ent. Soc. Lond., **1896** : 463.

Type: *superatalis*, Clem.

Hampson gives this generic name as a synonym of *Macalla* without giving reasons for it anywhere, except the general one that the genus is based on male characters only. He makes Section VA, *a*, for it, with male palpi similar to the female palpi; antennae of male with a long process from the basal joint, recurved over thorax and fringed with long hairs and scales below.

As a result of sinking *Epipaschia* as a synonym, Hampson later in the B.M. collection and in ms. notes discards the subfamily name and adopts the name POCOCERINAE.

In my paper, 1924, Bull. Hill. Mus., **1** : 502, I adopted this name, as I had not then had the opportunity to study the genotype more closely, naturally accepting the change on such a high authority.

Holland and Schaus, 1925, in Ann. Carnegie Mus., **16** : 49, attributed this change to me, which is not quite correct, though I may have been the first to publish the change. Had it been my change I would have given more full reasons for it.

I have now made a more detailed study of the genotype and have come to the conclusion that it may safely be regarded as a good genus, although the differences between this genus and *Macalla* are smaller than in *Lamida*, *Calomacalla* and *Teliphasa*.

The reasons given by Holland and Schaus for retaining this genus apart from *Macalla*, *l.c.*, p. 102, if applied to many other species might break *Macalla* and other genera up into much smaller groups than I am prepared to do at present, but, seeing that the genus has already been formed, I see no reason for lumping it with *Macalla*.

Description from *superatalis*.

Pl. XXX, fig. 23; Pl. XXXII, fig. 14; Pl. XXXV, fig. 12.

Male. In the venation I can see no difference worth recording, and even Holland and Schaus do not give any of generic value. Antennae with a long, rather *narrow*, sickle-shaped process (in *M. thyrsisalis* it is much broader and irregular in shape) covered with long hair mixed on the underside with scales. Labial palpi with the second joint solid, curved and twice first joint; third joint as long as first and sharply pointed. Maxillary palpi three-jointed; first joint minute, second and third joint sub-globular and covered with scales terminally. (In *thyrsisalis* the maxillary palpi have a long brush of hair, fitting in the cavity of the second joint of labial palpus.)

Genitalia : Uncus simple, moderately long, curved and provided at tip with hairs which point anteriorly; scaphium normal; vinculum of almost even width; valves shaped like a narrow oblique parallelogram, apex rounded, sparsely covered with hairs; juxta evenly chitinised and with some minute teeth at the tip; aedoeagus curved and pointed towards the tip; vesica without bristles. (In *thyrsisalis* the valves have a long process at base, the juxta has two processes and the aedoeagus has a corona of stout spines.)

Besides *superatalis*, Clem., I think we may also keep *Mochlocera zelleri*, Grote, here.

Epipaschia zelleri, Grote. Pl. XXXIV, figs. 8, 9, 10.

Male. Venation as in *superatalis* except that veins 10 and 11 are more remote from the stalk of 7, 8, 9. Process of antennae with many downwardly directed hairs on inner side in addition to the long scales; labial palpi with joint two over twice first joint; maxillary palpi with the joints narrower.

Genitalia almost as in *superatalis* but uncus less curved, vinculum much broader towards lower part, valves with a twisted projection on upper margin at one third, terminal margin more oblique, juxta with two tooth-like processes.

Epipaschia albomedialis, B. & B., placed by Holland and Schaus in this genus, is unknown to me from specimens, but the figure suggests that it is rightly placed here.

There is a possibility that *Macalla phaeobasalis*, Hmpsn., may have to come in *Epipaschia* (Pl. XXXIII, fig. 7) notwithstanding the fact that the genitalia are somewhat different and that the antennae have no process. Venation and palpi agree in every respect, but the basal joint of the antennae has a rounded-off bulge, the shaft is lamellate and fasciculate. Genitalia with uncus a little shorter, valves somewhat curved upwards; juxta with a curved, tooth-like projection; aedoeagus with two curved spines; penis as in *superatalis*.

Genus **Cecidipta.**

Cecidipta, Berg, 1878, Stettin. ent. Ztg., **39** : 230.
,, Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 468.

Type : *excaecariae*, Hmpsn.

Description from *excaecariae.*

Pl. XXIX, fig. 2; Pl. XXVIII, fig. 24; Pl. XXX, fig. 24; Pl. XXXIII, fig. 9.

The structure of my specimens differed so much from Hampson's description that I feared a wrong identification, although I had many specimens identified by different people. I consequently sent a specimen to the B.M. for verification, and Mr. Tams has kindly compared it with the series there, confirming my identification. As this species is rather variable in size and general appearance I made several dissections, but they all pointed to one species.

According to Hampson's key and description, both the fore-wing and hind-wing should have veins 4, 5 radiating, but my specimen shows approximation and in some cases even short stalking in the hind-wing and approximation in the fore-wing. The fore-wing should have vein 10 stalked with 7, 8, 9, but in all my specimens vein 10 is free though very close to the stalk of 7, 8, 9. The antennae are supposed to have only a tuft of hairs at base, but there is a distinct process; veins 3, 4, 5 of fore-wing are given from angle of cell, but 3 is from before the angle; in the hind-wing 3 is supposed to be from near and 4, 5 from lower angle but 3 is from well before angle and 4, 5 are approximated or even shortly stalked; veins 6, 7 are supposed to be from the upper angle but in reality they are shortly stalked.

I have *closely* examined 7 specimens and find that they all agree with the description following. The above inaccuracies clearly show that in many cases a superficial examination, without denuding the wings is rather misleading when laying the foundation of a classification, and much more so if the demonstration of relationship is attempted, as was done by Hampson in his paper.

Male. Fore-wing rather elongate; vein 3 from well before angle; 4, 5 closely approximated for one-fourth; 6 and stalk of 7, 8, 9 from upper angle; 7, 8, 9 stalked, 7 from one-third, 8 from two-thirds of 9; 10 free and from well before upper angle and running closely to stalk of 7, 8, 9; 11, 12 free. Hind-wing with vein 2 from two-thirds lower median; 3 from well before angle; 4, 5 shortly approximated or even stalked; 6, 7 shortly stalked; 8 free. Antennae with broad, rather short basal process, covered with long scales; shaft bipectinate for about one-third, pectinations very short, about thickness of shaft and each pectination fasciculate; remaining two-thirds of shaft lamellate and fasciculate. Labial palpi solid; second joint twice as long as first joint, curved and with a groove on inner side; third joint only one-third of first joint, rounded and with a small cavity. Maxillary palpi three-jointed, the joints cylindrical; joints 2 and 3 with tufts of long scales. Hind tibiae with two pairs of spurs.

Genitalia : Uncus moderate, broad towards tip, where it is curved, a row of short stiff hairs along the edge; scaphium well developed, ending in a hooked upcurved point; IXth sternite membranous, except along anterior and posterior margins; vinculum of same width all over, except towards end, where it is broadened, forming almost a saccus; juxta stout, well chitinised and forming two strong processes, which at base are attached to the vinculum; processes point upwards and towards each other; penis with an indistinct rod; aedoeagus short, rather thick towards end; valves rhomboid with the terminal points rounded off and the upper margin somewhat incurved.

In addition to the genotype Hampson places in this genus also *C. abnormalis*, Dogn., *Homura erythea*, Druce, and *Macalla paranensis*, Schaus. Of these I only have *erythea* (male and female types), and in these the venation agrees well with that of *excaecariae* except that the fore-wing has veins 4, 5 less approximated; the antennae have a process and the shaft has longer pectinations. The genitalia I have not been able to prepare yet, so I leave the placing of this species to the future.

Genus **Locastra.**

Locastra, Wlk., 1858, List. Lep. Ins. B.M., **16** : 158.
,, Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 469.

Type : *crassipennis*, Hmpsn.

Description from *crassipennis*.

Pl. XXIX, fig. 3; Pl. XXVIII, fig. 25; Pl. XXX, figs. 25, 26, 27; Pl. XXXIII, fig. 10.

The description given by Hampson does not define this genus sufficiently so as to exclude the others. In following the key, one would come to *Jocara* as vein 8 of hind-wing is not free, as given by Hampson, but connected with 7 by a bar, as shown in my illustration. I do not think this character sufficiently stable in the Epipaschiinae, however, for the grouping of genera.

The fore-wing has 3, 4, 5 from lower angle, but they are not quite from a point; the glandular swelling on costa causes the stalk of 7, 8, 9, 10, 11 to be somewhat curved there. Hind-wing has veins 4, 5 almost as remote as is the case with vein 3; 8 connected by a bar with 7 at one-third of vein 7.

Antennal process large, very broad at base, terminal two-thirds sickle-shaped, covered on the inside with long hairs and scales mixed; shaft laminate and fasciculate. Labial palpi upturned; second joint over twice as long as first joint, thickest at one-third, solid; third joint a little over half the length of first joint, tapering; joints one and two densely covered at front with long hairs and scales mixed, which in joint two are curled at the tip; maxillary palpi bifid as joint three is fixed to middle of joint two; both joints tufted with rather long scales.

Vertex of head with a short process, just behind each antenna and near the ocelli. This process I have not been able to find in any other Epipaschiines (Pl. XXX, fig. 26). It probably is homologous with the chaetosema found in other families, but in this case the structure was large enough to dissect it out and mount it on a slide. The tip is obliquely truncate and seems to be hollowed out; on the outside it is provided with a tuft of long scales. Fore tibia with two processes, one half the length of the other, both fairly hidden in the long hairs; hind tibia with two pairs of spurs.

Genitalia : Uncus moderate, straight, covered with stout hairs towards the tip; IXth sternite rather membranous and with the anterior and posterior edges well chitinised; scaphium rather long, very much curved and forming an upwardly curved hook at tip; vinculum very narrow and forming a saccus at base; two large coremata at base of valves consisting of long wavy hairs; juxta somewhat chitinised; aedoeagus and vesica without armature; valves pear-shaped, ending in a somewhat incurved point where there is a dense hair-bush; valves thinly covered with long hair; on lower margin a large number of short projections each with a few hairs on top.

In addition to the genotype the following species of *Locastra* have been studied by me, and though differing in some respects are possibly best placed here.

Locastra muscosalis, Wlk.

Fore-wing without fovea; hind-wing with vein 7 and 8 free; 6, 7 on a short stalk; otherwise the venation is as in the genotype. Antennae without process, basal joint only slightly swollen; palpi slightly different; no chaetosema; genitalia closely resembling those of *crassipennis.*

Locastra nocturnalis, Led.

Fore-wing without fovea; veins 6, 7, 8, 9 stalked; hind-wing with 6, 7 stalked; 8 anastomosing with 7; antennal process about three times as long as basal joint, bluntly pointed, covered with long scales; palpi very similar to those of *crassipennis,* but hairs shorter; fore tibia with one process only; no chaetosema. Genitalia almost as in *crassipennis,* but coremata absent; hairs on uncus longer and more abundant; valves broader and more densely covered with hair, and towards the apex the hairs become more abundant and longer.

At a later date perhaps a separate genus will have to be erected to include the American species.

Genus **Chloropaschia.**

Chloropaschia, Hmpsn., 1906, Ann. Mag. Nat. Hist., (7) **17** : 141.

Type : *thermalis*, Hmpsn.

Pl. XXVIII, fig. 26; Pl. XXIX, fig. 4; Pl. XXXIII, fig. 11.

Male. The specimen from which the description is made was identified by Dr. Schaus, and since he has the type female in his collection, I think that his identification must be correct. On the other hand, the structure of my specimen does not agree with the description in the following respects : in the fore-wing veins 4, 5 are not radiating from lower angle but are closely approximated for a short distance; 6 is not from upper angle but shortly stalked with 7, 8, 9; 10 is not stalked with 7, 8, 9 but free, forming a small areole by running very close along the stalk of 7, 8, 9; hind-wing has vein 6 not from upper angle but it touches 7 for some distance.

The palpi are as given by Hampson; unfortunately the third joint was lost in my preparation; the maxillary palpi are somewhat curved, as shown in Pl. XXVIII, fig. 26.

The genitalia are very peculiar in this group; the shape of the valves is very striking and not found in any other Epipaschiines. Uncus shorter than scaphium, straight, simple and terminally provided with long hairs, where the uncus is well curved; IXth tergite membranous with the edges strongly chitinised; scaphium ends in a long somewhat curved point; vinculum getting broader towards lower part; juxta (not shown in the illustration) shield-like, roundly tapering towards the tip; valves spoon-shaped, broad apical part almost circular, densely covered with long inwardly directed hairs and with a knob-like ridge at base covered with rather stiff hairs; aedoeagus rather short and slightly sinuate; no armature visible on penis.

I certainly consider this as a good genus in which I also place the following species :—

Chloropaschia (Macalla) granitalis, Feld.

Synonym : *Stericta contortilinealis*, Dogn.
Macalla rufilinea, Druce.

I have little doubt that *contortilinealis* is the same as Felder's *granitalis.* All structures, even the genitalia point to this, although the markings are sufficiently different to induce one to describe it as another species, when genitalia are not studied. This is another case which shows how essential such a study is.

One of my specimens of *contortilinealis* has a label in Hampson's handwriting, and in addition I have several specimens compared by myself at the B.M., so there can be little doubt about the identification. I have also the type of *M. rufilinea*, Druce, in my collection and, though considerably larger than the average *granitalis*, it is certainly the same as that species.

On the other hand, *granitalis* and *contortilinealis* are easily recognised as two separate forms by their markings. This species is certainly wrongly placed in *Macalla* or *Stericta.*

Pl. XXXIII, fig. 5.

Venation as in genotype except that the stalk of 6, 7 is only half the length of what it is there; palpi and antennae as in *thermalis* except that the maxillary palpus has the third joint a little thicker. The genitalia show such close affinity that it is difficult to find even specific differences. The shape of the scaphium is a little different, and the valve is less rounded and somewhat broader.

Genus **Stericta.**

Stericta, Led., 1863, Wien. Ent. Monats., **7** : 340.
,, Hmpsn., 1896, Trans. Ent. Soc. Lond., **1896** : 470.

Type : *divitalis,* Guen.

Pl. XXIX, fig. 5; Pl. XXX, fig. 28; Pl. XXXIII, fig. 13.

Lederer, when giving a new name to Guenée's genus *Glossina* (as that name was preoccupied), places here also, following Guenée, *habitalis,* Guen., which Hampson removed (rightly or wrongly I cannot say, for the species is unknown to me) to *Macalla.*

Lederer and Guenée consider vein 10 to issue from vein 9. Only females were known to them.

I have a female which agrees in every respect with the figure and description and also agrees with the specimens which the B.M. have under that name, but there are so many species that closely resemble it, that absolute certainty in assigning the male to it is not possible. However, I am fairly certain that the two males which I dissected belong to the same species as the dissected female, even though these specimens do not quite agree with the structures given by earlier workers, of which I consider Lederer as the most careful, but the species was not known to him from specimens. The female that I mainly use for the description is from Bidi (Sarawak); the male is from Admiralty Is.

When following Hampson's key one comes to *Stericta* only by assuming that vein 10 of fore-wing is quite free, but in my female 10 is free at base and then touches the stalk of 8, 9 so that a casual observation may make one think that it is stalked with 8, 9. In the male, however, that vein is quite free.

In other respects the venation agrees fairly well with Hampson's description, except that veins 4, 5 of both wings are a little apart and veins 6, 7 of the hind-wing are not stalked, but even a little apart.

Antennae (Pl. XXX, fig. 28) with a long rather slender sickle-shaped process densely covered, especially on the inner side, with scales. Labial palpi as in Pl. XXVIII, fig. 14, but first joint rather bigger, second joint less pointed at tip, third joint a little shorter and pointing forward. Maxillary palpi as in Pl. XXVIII, fig. 20, except that the first joint is shorter and the brushes on second and third joint are a little longer. In the female the labial palpi are as in Pl. XXVIII, fig. 2, and the maxillary palpi as in Pl. XXVIII, fig. 4.

Genitalia : Uncus as long as scaphium, simple, slightly incurved above and with terminal hairs directed forward; IXth tergite rather membranous, but edges well chitinised; scaphium sharply hooked at tip; vinculum rather narrow and of even width; juxta undeveloped; valves sole-shaped, moderately covered with hairs, more densely towards tip, which is rounded; penis rather small, apparently without any armature. (The preparations show no details, but it is possible that the bad position is responsible for that.)

For the present I keep only *divitalis* here, though I studied several species, including new ones, that will probably have to go here, but this must wait until more material is available. Many genera, sunk by Hampson in *Stericta,* however, *certainly* do not belong here and in many cases do not even show affinity. Those of which I have the genotypes will be dealt with here.

In ms. notes Hampson places *aleuropa,* Low., in this genus (in his section *Phiala*).

Genus **Craneophora.**

Craneophora, Christ., 1881, Bull. Soc. Nat. Moscow, **56**, (1): 2.

Type : *ficki,* Christ.

Pl. XXX, figs. 29, 30, 31; Pl. XXXV, figs. 13, 14, 15; Pl. XXXIV, figs. 1, 2, 3.

Description from *ficki.*

Male. The venation of the three species placed by me in this genus shows no great difference from that of *Stericta,* though the shape of the wings is less elongate. The only clear difference is that vein 11 and vein 10 *both* run very close to the stalk of 7, 8, 9 in *Craneophora,* while in *Stericta* vein 11 is quite remote from vein 10, and 10 is not quite so close to the stalk at base. All other characters, however, show these three species to be a compact group of generic status and the general appearance supports this. Undoubtedly the describer of the genus relied on this general appearance. It presents further a striking example of how insufficient venation *by itself* is, and how valuable male sexual characters are, *when combined with venation,* as guides when a natural classification is being attempted.

Antennae with a very long basal process, very densely covered with hairs and scales, which hide a great deal of the structure underneath. (In the illustration, Pl. XXX, figs. 29, 30, 31, this is shown after denuding them from most of the scales, leaving only those hairs and bristles which cannot be removed with slight brushing.) Apart from the irregular shape, the process shows a decided tendency to form two lobes terminally in the three species, and in *ficki* there appears to be a pointed claw at the end, absent in the other two species.

In *ficki* the covering of the process consists of rather short broad scales mixed, on the inner side particularly, with long hairs; some stiff hairs in between the others on inner side; shaft on outer side with small scales. Labial palpi upturned, second joint hollow and about four times as long as first joint and sparsely covered with scales and hairs, third joint acuminate and as long as first joint and thinly covered with hair. Maxillary palpi filiform, third joint tufted with long hairs. Spurs of mid tibia very long; two pairs of long spurs on hind tibia, outer spur two-thirds of inner one.

Genitalia : Uncus short and very broad; scaphium normal; vinculum moderate and of even width; juxta shield-like with two pointed projections; valve with a long stout spine from ridge near lower margin from before middle, followed by a short tooth-like process beyond middle and terminating ridge with another triangular projection; shape as in illustration, sparsely covered on inner side with long hairs; dense hairs on outer margin, but not forming a corona. Penis long and slender, without armature. A pair of coremata at base of IXth segment, also perhaps at VIIth segment, but here the hairs did not leave more than a trace of it.

Craneophora (*Stericta*) *carniola*, Hmpsn., 1916, Ann. Mag. Nat. Hist., (8), **18** : 146.

Pl. XXX, fig. 31; Pl. XXXV, fig. 14; Pl. XXXIV, fig. 2.

As will be readily seen from the illustrations this species is wrongly placed in *Stericta* and differs only in small details from *ficki*. The antennal process has a longer terminal lobe, the process is more curved and has on the inner side of the curve a series of stiff bristles. The labial palpi are the same, except that the third joint is thinner and a little longer. Maxillary palpi have joint three a little angled to two; first joint with a tuft of scales and third joint with a brush of hair.

Genitalia as in *ficki*, but lobes of uncus even broader; scaphium consists of two loose projections; juxta broken up into two portions; valve even more irregular, ridge more developed especially the terminal part, which is drawn up into a high ridge till past middle of valve; a lobe at lower angle; outer margin with a corona of rather short hairs, each hair having a little round knob on the end, suggesting a gland. Two *distinct* places on the abdomen where there is a pair of coremata, one pair at base of VIIth and one at IXth segment. (The hairs came off in the preparation.)

Craneophora (*Stericta*) *haraldusalis*, Wlk.

Male. Antennae with the process very similar to *carniola*, but terminal process not quite so long and also provided with a large number of stiff bristles on inner side; the whole process is well covered with hairs and broad scales, especially on the inner side and towards the end. Labial palpi as in preceding species; maxillary palpi with the joints as in *carniola*, but hairs of joint three spreading in all directions.

Genitalia: Uncus, scaphium and juxta as in *carniola*; valves shorter and less lobed than in that species; outer margin also with a long corona as in *carniola*, but along the whole edge and with only a few "glandular" hairs on upper half. At base of IXth and VIIth segment a pair of coremata.

From all this it will be easily seen that this group is of generic status and that there is no reason for sinking it under *Stericta*, with which it has only the neuration *somewhat* in common.

Genus **Sarama**.

Sarama, Moore, 1888, Lep. Atk., p. 203.

Type: *atkinsoni*, Moore.

Pl. XXXIV, fig. 7; Pl. XXXVI, figs. 15, 16.

The description is made from a specimen derived from the Atkinson collection and with a ms. label on it with the name *Sarama atkinsoni*. It was also found by me to be identical with the type in the B.M., so I am fairly sure that it is correctly identified. Though Hampson sunk this genus under *Stericta* and although here too the venation is very much as in *S. divitalis*, yet I think it should be kept distinct owing to other points in its structure.

Male. Fore-wing with veins 6, 7 shortly stalked; 10 runs very close to stalk of 7, 8, 9, and only diverges from it to beyond where 9 comes from 8. Hind-wing with veins 6, 7 shortly stalked. In all other respects the venation is the same as in *divitalis*, and I certainly think that this stalking of 6, 7 in both wings is unimportant, *unless supported by other characters.*

Antennae with a large curved process, more resembling that of *Craneophora* than of *Stericta*; a blunt rounded tooth at one-third; process strongly curved a little beyond middle and covered with dense hairs and scales mixed, especially on the inner side of the curve; shaft fasciculate. Labial palpi upturned, sharply angled at first and second joint, second joint five times first joint, tapering to a point, hollow and slit over the whole length as in *S. divitalis*; third joint shorter than first joint, thin, acuminate; first and second joint thinly covered with scales, third joint with short hairs. Maxillary palpi three-jointed, joints cylindrical, second joint over twice first joint, third joint inserted on second joint at one-fourth and very thin; second and third joint each with a brush of long hair.

Genitalia: Uncus long, curved and ending in two prongs which almost form a semicircle, prongs with short hairs on inner side; IXth tergite broad, membranous, broadly chitinised posteriorly and narrowly anteriorly; scaphium rather short and broad, ending in a strong upcurved point; vinculum rather narrow and of even width; valves elongate, upper and lower margin parallel, outer margin at right angles, inner margin very oblique; a broad, curved irregular process on upper inner angle; lower half of valve somewhat raised, thickened and most densely covered with hair; remainder less dense.

No other Epipaschiines have been found by me with such peculiar genitalia, and though there is certainly a close affinity to *Stericta* and *Craneophora*, yet I consider this a distinct genus.

Genus **Leptosphetta.**

Leptosphetta, Butl., 1878, Trans. Ent. Soc. Lond., **1878**: 67.

Type: *rabdina*, Butl. = *scopipes*, Feld.

Hampson gives this name to a subdivision of *Stericta*, but for reasons given below I consider this a good genus. Butler places it in the NOTODONTIDAE, which shows clearly that the structural characters cannot have been studied by that author in very great detail; in fact the description given by him, though fitting in all respects, does not give the least clue to its real position.

According to Hampson it has all the general *Stericta* characters plus the fact that the antennae have no process and that the hind tibiae have a large brush of hairs. This is not quite true, as in the hind-wing veins 4, 5 are well stalked, while vein 3 comes from near the stalk; in the fore-wing vein 3 comes from well before angle; 6 is shortly stalked with 7, 8, 9.

Antennae with a very short process. The genitalia come very close to those of *S. divitalis*, but as the venation is quite different and secondary male characters are different too, I think it should be kept distinct, though it has closer affinity with *Stericta* than the general appearance would suggest.

Male. Description made from *scopipes*, Feld., which, according to Hampson, is the same as Butler's *rabdina*.

Fore-wing rather narrow and long; vein 3 from a little beyond 2; 4, 5 from lower angle; discocellulars very much curved inwardly; 6 shortly stalked with 7, 8, 9; 7 from one-third, 8 from two-thirds of 9; 10 from before upper angle, parallel with stalk and almost touching 9; 11 from two-thirds upper median and in the middle almost touching vein 10; on underside a large patch of androconia in and beyond cell. Hind-wing broad, triangular and with a large patch of androconia in centre of wing; vein 2 from beyond middle of lower median; 3 from just before lower angle; discocellulars very oblique and straight; 4, 5 with a stalk of over one-fourth and from lower angle; 6 shortly stalked with 7; 8 curved upwards above upper median, then curving downwards to vein 7 and almost touching it. Antennae with a basal conical swelling as in Pl. XXX, fig. 4; shaft fasciculate; labial palpi upturned, very much as in Pl. XXVIII, fig. 18, but first and second joint a little more angled and third joint even shorter; maxillary palpi as in Pl. XXVIII, fig. 16*a*. Fore legs with process on tibia; mid legs with tuft of hairs on tibia and first tarsal joint; hind legs with tuft of long hairs on tibia and first tarsal joint and two pairs of spurs, which are rather close together as tibia is much shorter than first tarsal joint.

Genitalia very much like those of *S. divitalis*, Pl. XXXIII, fig. 13, but uncus with larger area covered with hair; juxta well represented; valves a little broader and with an oblique ridge near base; tip with more and longer hairs; penis longer, stouter and straight; aedoeagus with a slit at tip and probably with a spine; vesica without armature.

Leptosphetta (*Stericta*) *abrupta*, Zell.

Venation just as in *scopipes*; on hind legs I cannot find a trace of median spurs, however, while the tufts of hair are even thicker and longer and the spines on the first tarsal joints are very long; shaft of antennae with longer fasciculate hairs. Genitalia as in *scopipes*, but valve with an additional basal ridge at lower margin.

I have no doubt that these two are good species, although the genitalia run very close.

This genus is probably confined to America, and no other species are known to me.

Genus **Orthaga.**

Orthaga, Wlk., 1858, List. Lep. Ins. B.M., **16** : 191.

Type : *euadrusalis*, Wlk.

Pl. XXIX, fig. 6; Pl. XXXIII, fig. 12; Pl. XXXV, fig. 1.

Description from *euadrusalis*.

I suspect this genus also to contain several genera and a number of the synonyms will no doubt have to be re-established. Lack of genotype material prevents me from dealing with this matter fully, but I hope to do so at a future date. For the present I confine myself to what I consider to be the true *Orthaga*.

Male. Fore-wing with a glandular swelling on costa at middle, and as a consequence of this the venation is rather modified, as can be readily seen in the illustration. Veins 2, 3 from near lower angle; 4, 5 shortly stalked and from lower angle; 6 from near upper angle and very much curved downwards so as almost to touch vein 5; 7, 8, 9 stalked, stalk curved and swollen along the gland; 10 slightly curved and also swollen at gland; 11 passes through middle of gland, where it is strongly sinuate; 12 abruptly ends at gland. Hind-wing with vein 3 from near lower angle; 4, 5 somewhat approximated to each other; an indication of a bar between 7 and 8; 8 not quite touching 7.

Antennae without process at basal joint, though first joint is somewhat swollen; shaft serrate and fasciculate. Labial palpi upturned, solid; second joint a little longer than first joint; third joint about half length of second joint, sharply pointed. Maxillary palpi three-jointed; joints two and three somewhat at an angle and tufted with scales. Fore tibia with a process; mid tibia with long spurs; hind tibia with long hairs and two pairs of spurs.

Genitalia : Uncus long, straight and broad at tip and with a row of stiff hairs; scaphium normal; vinculum very narrow, long and oblique, broadest at base, where there are two coremata with hairs almost as long as the valves; juxta simple, membranous; valves sole-shaped; upper and lower margin parallel, basal and outer margin very oblique, point rounded and somewhat upcurved; penis simple, straight.

The specimen from which the description is made was from Sumatra (Fort de Kock), and was carefully compared for me by Mr. Tams with the type, in order to make sure of my identification.

Orthaga (Pannucha) basalis, Moore.

Pl. XXXVI, fig. 12.

Through the kindness of the Berlin Zoological Museum I have been able to examine the type of *basalis* and make a preparation of the genitalia, which is now in that museum. All structural details point to such close affinity with *Orthaga* that I do not think it advisable to keep it in a separate genus. The main difference is, that the antennae have a short process, the vesica has a stout spine and an area covered with very small spines. The fore-wing has vein 10 very shortly stalked with 7, 8, 9, but otherwise the venation is the same. The labial palpi are solid, as in Pl. XXXV, fig. 1; maxillary palpi are triangularly scaled. Fore tibia with a process and hind tibia with two pairs of spurs.

Orthaga jucundalis, Wlk.

Pl. XXXVII, fig. 4.

This species is better placed in *Orthaga*, and is certainly not a *Stericta*; the palpi are much too small for that, and other structures point to this position as well.

Antennae without a process; palpi as in genotype, but less curved; venation almost as in genotype, but glandular swelling somewhat further from the costa; tibia with scales and some long hairs; hind tibia with 4 spurs.

Genitalia very similar to those of genotype except that the lower margin of the valve is provided with a beautiful dense fringe of large broad scales not found by me in any other Epipaschiines.

Orthaga exvinacea, Hmpsn.

Pl. XXXV, fig. 21; Pl. XXXVI, figs. 13, 14.

The specimen studied by me is from Ceylon and agrees very well with the genotype in structure. In this species the palpi are more curved, especially the second joint; the third joint is less acuminate. The legs are less hairy; the glandular swelling of the fore-wing has influenced the venation less. In the genitalia the vinculum is broader, shorter and less oblique and the coremata are smaller; the aedoeagus seems to have a tooth near the extremity and the penis is curved in the middle; the valve is a little narrower, but otherwise the same.

Genus **Islopha.**

Islopha, Hmpsn., 1895, Ann. Mag. Nat. Hist., (6) **16** : 346.

Type : *lactealis*, Hmpsn.

The type is not known to me, but I have a female of *albicristata*, Warr., which Hampson himself places in this genus.

Description from *Islopha albicristata*, Warr.

Pl. XXIX, fig. 7; Pl. XXXV, fig. 16.

Female. The venation of this female agrees with Hampson's description except that the hind-wing does not have veins 4, 5 approximate. The antennae are not simple, as even those of the female are bipectinate and the basal joint is somewhat enlarged and has a tuft of long scales. Fore tibia with a process; mid and hind tibia covered with hairs and scales mixed; hind tibia with two pairs of spurs. Labial palpi porrect, rostriform, second joint two and a half times first joint and with long scales above and below; third joint half length of second joint, much thinner, pointed and hidden in scales; maxillary palpi triangularly scaled.

A study of the males of the two species may quite well show that the African species should not be placed here.

Genus **Polylophota.**

Polylophota, Hmpsn., 1906, Ann. Mag. Nat. Hist., (7) **17** : 189.

Type : *barbarossa*, Hmpsn.

Besides the genotype two other species are placed here by Hampson, namely *truncalis*, Kenr., and *arruensis*, Kenr., the latter of which is unknown to me.

Description from genotype.

Pl. XXX, fig. 32; Pl. XXXV, fig. 17; Pl. XXIX, fig. 8; Pl. XXXIV, fig. 4.

Male. In following Hampson's ms. key one would not come to this genus, as vein 10 is quite free, but, owing to the glandular swelling this is not easy to see without making a preparation. According to the description the antennae are supposed to have a tuft of hair only, but in reality there is a process; the hind-wing is supposed to have veins 7, 8 free, but there is a distinct bar, which is not mentioned; the fore-wing is supposed to have 4, 5 well separate at origin, but they are shortly stalked and veins 2, 3 are from a point, although in *truncalis* they are remote; no glandular swelling is mentioned for the hind-wings, though it is present in both species.

Antennae with long pointed process, covered with long scales; labial palpi upturned, second joint over twice length of first joint, covered with dense long scales; third joint very small, hidden in scales; maxillary palpi tufted with long scales.

Fore-wing with veins 2, 3 from a point, well below lower angle; 4, 5 on a short stalk and from lower angle; discocellulars obliquely angled; 6 from below upper angle; 7, 8, 9, stalked and from upper angle; a glandular swelling between stalk of 7, 8, 9 and costa; 10 close along stalk of 7, 8, 9 and then diverging beyond the gland; 11 through the gland; tuft of hairs and scales from cell on upperside. Hind-wing with vein 3 from far before lower angle; 4, 5 remote and from lower angle; lower discocellular oblique and long, upper one very short; 6, 7 stalked and from upper angle; 8 connected with 7 by a bar; inner margin with a large tuft of very long hair; an oval glandular patch, crossed by lower median, in cell.

Genitalia: Uncus rather short and broad, terminating in a row of stiff bristles; scaphium normal; vinculum of even width; valve somewhat tapering, point rounded, covered with long hair; juxta membranous; penis rather short; aedoeagus with a spinous process at tip.

I have no doubt that this is a good genus.

Polylophota truncalis, Kenr., 1907, Proc. Zool. Soc. Lond., **1907**: 72.
Pl. XXIX, fig. 23.

Process of antennae present, but a little shorter; palpi as in *barbarossa*. Fore-wing with veins 2, 3, 4 apart and at equal distance; 4, 5 at half that distance, 6 equidistant from 5 and 7; 7, 8, 9, 10 stalked and from upper angle, though I think that the stalking of vein 10 is really due to the glandular swelling at costa; 11 and 12 as in previous species; a large tuft of long hair from near upper median far over lower median. Hind-wing as in *barbarossa* except that vein 8 is anastomosing with 7 and is not connected with that vein by means of a bar, as is the case there.

Genitalia as in *barbarossa*, but the uncus a little curved; valve more sickle-shaped; penis a little longer and thinner; on aedoeagus a dark portion is visible that may be a process similar to that found in *barbarossa*, but I cannot make it out with certainty.

Judging from the illustration it is quite possible that *arruensis* belongs here too, as the general appearance of the two foregoing species is certainly typical for the genus.

Polylophota senilis, sp. n.

Pl. XXXVII, fig. 6.

Male and female. Head, thorax, abdomen and wings with ground-colour whitish-yellow; head and thorax well irrorated with ferruginous (xvi); fore-wing with basal area densely irrorated with ferruginous defined by a dense clouding of fuscous (xlvi) from one third of costa to well before middle of inner margin, where the clouding is rather broad and preceded by whitish scaling and angled inwardly at vein 1*b*; some dark semilunar scaling defines it to a white line; median area with white scales, except at costa at middle, part of the cell and inner marginal area beyond middle, where there is a dense clouding of ferruginous, mixed with fuscous scales; postmedial line fuscous, narrow, well defined on the white background, zigzagged inwardly between the veins; a terminal border of ferruginous mixed with white scales on veins 3–7; towards apex the ferruginous is mixed with darker scales; terminal line represented by fuscous lunular marks between the veins; cilia yellowish with ferruginous scales mixed and having a dark line across them. Hind-wing whitish, except along the costa, where there is a sprinkling of ferruginous; cilia as in fore-wing, but lighter in colour; inner margin with long yellowish hairs.

Underside: Fore-wing and hind-wing with whitish ground-colour; fore-wing densely irrorated with ferruginous over the whole area except along inner margin and just beyond postmedial line, which is well defined with fuscous; a terminal series of fuscous elongated spots. Hind-wing narrowly irrorated with ferruginous and yellow scales mixed along costa; a terminal series of elongate ferruginous spots; abdomen irrorated with ferruginous.

Female marked like male.

In some specimens the basal and terminal irroration is well mixed with yellowish scales.

Exp. in male, 40 mm.; in female, 43 mm.

Hab. Types: male and female, from Angi lakes, Arfak Mts. (North New Guinea), 6000 ft., collected in March 1914 by A. C. and F. Pratt. Cotypes: three other males and three females from the same locality, collected in Jan., Febr. and March 1914.

The male fore-wing has the normal glandular swelling; vein 10 is free at base, but in the gland it anastomoses with the stalk of 7, 8, 9; 6 is far from the stalk; 4, 5 are very shortly stalked and come with 3 from lower angle; 2 is from far before the angle. Hind-wing with no glandular patch; 3 from one-fourth of vein 2 to lower angle; 4, 5 from lower angle; 6, 7 on a stalk as long as lower discocellular; 8 anastomosing with 7 for nearly length of that stalk. Spurs with bristle-like hairs. Antennae rather short and blunt; palpi as in genotype.

Genitalia as in genotype, but uncus shorter; scaphium more curved; valves narrower beyond middle; penis also with a spinous process, which is slightly shorter.

Polylophota (*Locastra*) *atriplagalis*, Hmpsn.

Fore-wing with a fovea; vein 10 is not quite free as it joins stalk of 7, 8, 9 at the fovea, veins 4, 5 well stalked; hind-wing with 6, 7 well stalked and 8 anastomosing with 7.

In using Hampson's key, as far as published, for placing this species one would come to *Jocara* and *Astrapometis* as it agrees with these genera in vein 6, 7 and 8 of the hind-wing, but in the fore-wing veins 4, 5 would have to be separate and no fovea should be present. In *Astrapometis* the antennal process is much shorter, but the palpi would agree fairly well. The genitalia also agree somewhat with *Astrapometis*. Labial palpi as in *L. nocturnalis*: maxillary palpi triangularly scaled; antennal process short, thick and very densely covered with scales; fore tibia with one process. Genitalia very similar to those of *P. barbarossa*, but uncus a little shorter, aedoeagus without process; juxta somewhat chitinised; valve even more curved and narrowed to half beyond middle, whence it remains of even width until it forms a rounded point; penis rather long; vesica covered with very short spines.

I have one other new species, which has to come here, but which I shall not describe until I have more and better material. This too is from Buru and New Guinea, so that it seems that this genus is confined to the Indo-Australian sub-region.

Genus **Taeniaphora.**

Taeniaphora, Kenr., 1917, Trans. Ent. Soc. Lond., **1917** : 97.

Type : *submarginata*, Kenr.

In Hampson's ms. key vein 10 is given as stalked with 7, 8, 9 for this genus, but Kenrick does not mention anything about this vein. As I have a specimen kindly presented to me by Sir Geo. Kenrick (one of the series which he used in the description), I am quite certain of the identification, and in this specimen vein 10 is quite free. So I now give a fuller generic description from that specimen.

Pl. XXXV, fig. 18; Pl. XXX, fig. 33; Pl. XXIX, fig. 9; Pl. XXXIV, fig. 5.

Male. Palpi porrect, rostriform; second joint three times as long as first joint, covered with long hair-like scales above and below; third joint half the length of the second joint, tapering and covered with short hairs; maxillary palpi three-jointed; third joint longest and angled to second joint; second joint with a tuft of long scales below; third joint with a tuft of hair.

Antennae with first joint globular and with a tuft of long scales and hairs mixed; shaft shortly bipectinate, each branch fasciculate with long cilia. Hind legs: my specimen has no hind legs, so I do not know whether it has one or two pairs of spurs; Kenrick states that it has the tibiae with fairly long spines, but, as the mid tibiae of my specimen are well covered with scales I think this must also have been the case with the hind legs, and then spines would have been difficult to detect; so I am fairly sure that "spines" is a misprint for spurs, which are certainly quite long in the mid tibia.

Fore-wing with vein 3 midway between 2 and 4; 4 and 5 remote; 6 and stalk of 7, 8, 9 remote; 7, 8, 9 stalked; 10 from halfway between stalk of 7, 8, 9 and vein 11, slightly approximating the stalk of 7, 8, 9, but quite free; 11 parallel with 10. Hind-wing with 3 nearer 4 than 2; 4, 5 remote; 6, 7 almost from a point; 8 approximated to 7.

Genitalia: Uncus curved inwards at base, then straight and covered over the whole length with hairs; IXth tergite fairly well chitinised; scaphium rather short, stout and ending in a curved point; vinculum rather broad, broadest at base; valves rather short and broad and with a number of striae from outer margin to base and covered with fairly long hairs; penis gently curved, as long as the valves and without armature.

Only one species known in this genus.

Genus **Rhynchopaschia.**

Rhynchopaschia, Hmpsn., 1906, Ann. Mag. Nat. Hist., (7) **17** : 190.

Type : *melanolopha*, Hmpsn.

This genus was erected by Hampson on a species of which a female was collected in Mashonaland, and the description agrees in every respect with specimens in my collection, also from Mashonaland and the Northern and Eastern Transvaal. When comparing my specimens with the type in the B.M. I found them identical in every respect, except that my largest specimen is only 23 mm. However, on coming to South Africa again and studying the structural characters, I found they did not agree with the generic description in some important respects. The hind-wing has vein 1*c* absent, 6, 7 are shortly stalked and not from upper angle as given. (This, however, may vary to some extent, though all specimens examined by me are stalked.) Vein 7 of fore-wing is *absent* and not from beyond 9, as Hampson states. (This, however, is difficult to make out unless a preparation is made.)

Except for the absence of 1*c* in hind-wing and vein 7 in fore-wing the description fits my specimens quite well as far as it goes, and seeing that Hampson made no preparation of the wings I am sure that these details must have escaped him. So I am sure of the identification, and it may be possible that it does not belong to the EPIPASCHIINAE at all, seeing that 1*c* is missing and that the scaphium is absent, but I cannot offer a better position for this genus at present, and look upon it as one of the most reduced groups. I thus re-describe it from a male specimen.

Pl. XXIX, fig. 10; Pl. XXXV, fig. 19; Pl. XXXIV, figs. 6, 6*a*.

Male. Antennae without a process; shaft minutely serrate and fasciculate; labial palpi porrect, second joint thick and about four times length of first joint, thinly covered with scales; third joint drooping, as long as first joint, thick, cylindrical, covered with hair-like scales. Maxillary palpi four-jointed; first three joints very small, fourth joint egg-shaped and as long as the three others together and somewhat set at an angle and covered with a long tuft of scales. Fore tibia with a process and tufted with hair; mid tibia with terminal spurs; hind tibia with two pairs of spurs.

Fore-wing: 1*c* forked and with a spur towards the margin; 2 from two-thirds of lower median; 3 from two-thirds vein 2 to lower angle; 4, 5 on a stalk a little less than one-fourth; 6 from below upper angle; 7 absent; 8, 9 stalked for about half of 9 and from upper angle; 10 from well before angle and remote; 11 parallel with 10.

Hind-wing: 1*c* absent; 2 from two-thirds lower median; 3 from beyond middle of vein 2 to lower angle; 4, 5 shortly stalked or from a point and from lower angle; discocellulars oblique, curved; 6, 7 on a short stalk and from upper angle; 8 anastomosing with 7 for one-third of that vein.

Genitalia: Uncus very short, simple and covered with short hairs; below it two rounded lobes, suggesting the remains of a scaphium; scaphium absent; IXth tergite well chitinised and of even width; vinculum like tergite but getting broader and pointed towards base;

valve bifurcate at base, then narrowing down to a width equal to half its length when the upper and lower margins become parallel; outer margin inwardly oblique; a short process on inner side near upper margin at one-third; valves covered with many stout hairs; penis rather short, thickened towards tip; aedoeagus with a terminal protuberance covered with stout hooks.

Rhynchopaschia reducta, sp. n.

Pl. XXXV, fig. 20; Pl. XXIX, fig. 11.

This species shows, without doubt, many generic points of difference from the genotype, but until more species are known I think it better to place it here for the present.

It differs in the following characters: labial palpi with the third joint thin and in line with joint two; maxillary palpi with three joints, third joint smaller and thinner; hind-wing with vein 3 absent; 4, 5 somewhat remote, 6, 7 from a point; genitalia without the lobes on the tergite, valves shorter and broader at the narrowest part, apex rounded, penis shorter and thicker, aedoeagus with protuberance smaller.

Male and female. Head, thorax and abdomen covered with fuscous-black scales; palpi with metallic bluish scales; fore-wing with broad basal third irrorated with fuscous and fuscous-black scales mixed, obliquely from near middle of costa to one-third of inner margin, where there are some long blackish projecting scales; median area well irrorated with white scales, except for two tufts of long black scales in cell before and almost beyond it; terminal area irrorated with fuscous, blackish and reddish scales mixed, except towards apex and near outer margin, where there are also white scales mixed with it; a subterminal row of three orange-yellow maculae, largest between veins 1*b* and 2, smallest between veins 4 and 5; cilia grey with white and black scales mixed, forming a dark line over the middle of it. Hind-wing and its cilia grey with fuscous irroration.

Underside: Both wings grey with fuscous-black irroration; fore-wing with iridescent bluish scales along inner marginal area.

Exp. in male, 14 mm.; in female, 18 mm.

Hab. Type: male, Barberton, 7.xii.1910; type: female, Pretoria, 3.xii.1915.

Several other specimens from the same localities and from Chuniespoort, Tzaneen, Mahuba's Kloof, Potgietersrust, Buffelspoort (Transvaal); Umkomaas (Natal), Bulawayo (Southern Rhodesia), all in December, January and February.

Genus **Doddiana.**

Doddiana, Turn., 1902, Trans. R. Soc. S. Australia, **26**: 187.

Type: *callizona*, Low.

I have a rather poor female specimen in my collection, and I have to leave a fuller description till more material comes to hand; meanwhile Pl. XXXVI, fig. 1, and Pl. XXIX, fig. 12, give the details that I have been able to make out so far.

Here too vein 7 of the fore-wing is absent, but vein 10 is stalked with 8, 9. The hind-wing has all the required veins, and the palpi are very similar to those of the previous genus.

Genus **Paranatula.**

Paranatula, Dyar, 1913, Proc. U.S. Nat. Mus., **44**: 321.

Type : *zographica*, Dyar.

The specimen used for dissection was kindly identified for me by Dr. Schaus, so I have no doubt that the identification is correct.

Pl. XXIX, fig. 13; Pl. XXX, fig. 34; Pl. XXXVI, figs. 2, 3.

Male. Antennae with a long sickle-shaped basal process, thinly covered with scales (this is probably the structure that Dyar described as *palpi* with a long thick basal process); shaft biciliate; labial palpi upturned, solid; second joint over twice length of first joint; third joint a little shorter and acuminate; first joint with a tuft of scales below; the other two joints smoothly and thinly covered with scales; maxillary palpi three-jointed, the joints about equal in size and similar in shape; joint three at right angles to second joint; second joint with a tuft of a few hairs; third joint with a larger tuft of hair like scales. Fore-wing with vein 1*b* simple; vein 3 from near middle of vein 2 and lower angle; 4, 5 approximated for nearly half their length and from lower angle; vein 6 and stalk of 7, 8, 9 from upper angle; 7, 8, 9 on a stalk of nearly half length of 7; 10 approximated to stalk of 7, 8, 9. Hind-wing with vein 3 from beyond middle of vein 2 and lower angle; 4, 5 on a stalk of nearly half; 6 stalked with 7; upper median indistinct; 8 anastomosing with 7 for some distance. (My specimen has lost both its mid legs and the hind legs have only terminal spurs. As some repairing has been done to the specimen there is a possibility of error even in that.)

Genitalia: Uncus simple, rather broad and with stiff hairs at the tip; IXth tergite rather membranous except on the edges, which are well chitinised; scaphium well developed, very much curved, suddenly getting thicker near the tip and ending in a well-hooked point; vinculum narrow, of even width and ending in a saccus; valve narrowly sole-shaped, rounded at tip, where the hairs are more dense than over the remainder; penis rather short; aedoeagus with a number of short spines.

In addition to *zographica*, Dr. Schaus also places here *costata*, Schaus, *colorata*, Dyar, and *vincentia*, Schaus, all from Central America. The latter three species I have not been able to study.

Genus **Pocopaschia.**

Pocopaschia, Dyar, 1914, Proc. U.S. Nat. Mus., **47** : 324.

Type : *noctuina*, Schaus.

Description made from a specimen identified by Dr. Schaus.

Pl. XXIX, fig. 15; Pl. XXXVI, figs. 6, 9.

Male. Antennae without a process; shaft shortly bipectinate, pectinations ciliated; labial palpi very peculiar, as Dyar describes, but the modified claw-like third joint looks like an outgrowth of the second joint as it shows no join at all. In fig. 9 it is shown from the inside as well as from the outside. I have not been able to find the maxillary palpi, and they may be absent. Fore-wing with vein 3 from two-thirds of vein 2 and lower angle; 4, 5 on a stalk of one-third and from lower angle; 6 from before upper angle; 7, 8, 9, 10 stalked and from upper angle; 11 parallel with 10 and stalk. Hind-wing with vein 2 from three-fourths lower median; 3 remote from lower angle; 4, 5 on a stalk of half of vein 5 and from lower angle; 6, 7 on a short stalk; 8 anastomosing with 7 for nearly half length of 7.

Genitalia very peculiar and suggesting that this species does not belong to the EPIPASCHIINAE at all. Uncus broad at base as a direct continuation of the broad IXth tergite, then gradually tapering and provided with two small terminal hooks; tip of uncus covered with hairs for nearly half its length; scaphium absent, or perhaps represented by the two lateral, pointed processes found very low down near the base of the valves (these processes may, however, also represent the juxta and are certainly in the right place for it); sternite broad and widening backwards and forwards at base; valves rather small, sole-shaped, rounded at apex and covered with short hairs; penis short and thick; aedoeagus with four or five stout spines (not shown in figure).

Two other species are placed in this genus (both from Central America), *accelerans*, Dyar, and *bellangula*, Dyar; the former has vein 7 from stalk before vein 9, the genotype and *bellangula* have 7 from beyond 9; in *noctuina* the hind-wing has vein 3 from the cell, while *bellangula* has that vein stalked with 4, 5. Only *accelerans* is known to me from a specimen, and the one in my collection, a male, unfortunately has the abdomen missing. The venation is as given by Dyar (Pl. XXXVI, fig. 6) and the labial palpi (Pl. XXXVI, fig. 8) certainly shows strong affinity with the genotype, but here the three joints are quite distinct; first joint cylindrical and with a brush of scales on the underside; second joint cylindrical but tapering on upperside into a long point and provided with dense scaling on underside; third joint practically naked, narrowed at one-third, terminal half thickened and then tapering into an oblique point; a deep cavity before the tip at the front.

Genus **Coenodomus.**

Coenodomus, Wlsm., 1889, Trans. Ent. Soc. Lond., **1889** : 49.

Type : *hockingi*, Wlsm.

Pl. XXXVI, figs. 10, 11.

The description given by Walsingham is quite full and accurate, including even a fairly good description of the genitalia. Hampson's description does not, however, fit in with the genotype in every respect and is perhaps made to fit the other two species included by that author and unknown to me from specimens; the figure given by him is that of *hockingi*.

The labial palpus has the second joint not hollowed out to receive brush-like maxillary palpi, that joint being solid and the maxillary palpi triangularly scaled, though the scales are fairly long. Fore tibia with a long outwardly curved process; hind tibia with two pairs of spurs, the outer spur shortest; fore-wing with veins 8, 9 on a long stalk; hind-wing with 6, 7 shortly stalked in male, but free in right wing of female and with a little cell at base in left wing (this shows how little one can rely on such short stalking, even when it is present in a number of specimens); 7, 8 free in male but in left wing of female 8 is just touching and in the right wing quite free.

A peculiar feature in the hind-wing of the male is that vein 7 of both wings is branched for about one-third of its length giving the impression that there is an additional vein, which is stalked with 7. In the female 7 is normal, but the right wing has a branch coming from 8 well before it approximates 7. As only two specimens were studied, I do not know how often this abnormality can be expected to occur in this species.

Genitalia : Uncus very broad, rather short and shortly bilobate and densely covered with short hairs over the whole length and with a fringe of rather long hairs along the edge; IXth tergite somewhat membranous, but chitinised along anterior edge; scaphium short, stout and ending in a sharp point; vinculum rather narrow and of almost even width; valves half-moon shaped, rather broad and with rounded apex, moderately covered with hair, which becomes more dense towards the apex; penis much curved at one-third, then almost straight; no armature on penis or aedoeagus; saccus absent.

The specimens studied were kindly loaned by the Berlin Zoological Museum, where the preparations are also deposited. I am not sure about the affinity of this genus; according to the venation it may come in the neighbourhood of *Orthaga* and *Locastra*, but other structures do not seem to confirm this view.

Plumiphora, gen. n.

Pl. XXXVII, figs. 1, 2, 3; Pl. XXXIV, figs. 11–15.

Type: *pratti*, sp. n.

Male. Antennae with a very long process, curved below middle and getting thicker terminad; on inner side of curve various sets of long scales mixed with hairs; a spreading series of curled hairs terminally; shaft bifasciculate; labial palpi very long, but apparently of two joints only, second joint over six times length of first joint; second joint curved at base, hollow over the whole length to receive a brush, moderately covered with scales; maxillary palpi three-jointed; second and third joint almost from a point and angled to first joint; second and third joint with a tuft of very long straight hairs. Fore-wing with vein 2 from two-thirds lower median; vein 3 beyond middle of vein 2 and lower angle; 4, 5 from lower angle and approximated for a short distance; 6 from below upper angle; 7 stalked with 8 for one-eighth; 9 from 8 at four-fifths of 8; 10 free but very close to stalk of 8, 9; 11 free. Hind-wing with vein 3 from near lower angle; 4, 5 from lower angle and approximated for some distance; 6, 7 from upper angle; 8 approximated to 7 but still free. Hind tibia with median spurs from one-third, long; terminal spurs shorter and a little curved; tibia and first tarsal joint each with a tuft of long hair.

Genitalia extremely peculiar, yet having all the essentials of this subfamily. Uncus very short and ending in a blunt point (in fig. 13, *sc* is the scaphium, *u* the uncus and *v* the valve); IXth tergite strongly chitinised and of even width; vinculum broad, well chitinised; juxta well chitinised, but I cannot make out the correct shape of it, in the only preparation; scaphium present but short and ending in an abrupt point; valves directed obliquely upwards, narrow, pointed and rather irregular in shape; point of valves ending in a sharply pointed process, inner side of valve sparingly covered with hair, except towards the tip, where there is a fringe of hair-like scales; penis rather short, very thick towards apical half, where the aedoeagus is very heavily chitinised and provided with knobs and rough ridges, which differ on each side (fig. 14 shows this from one side, fig. 15 from the opposite side).

According to venation this would come somewhere near Hampson's *Macalla* group, yet there are far too many structural differences to accommodate the genotype in that group, while in general appearance the species seems to belong to *Stericta*.

Plumiphora pratti, sp. n.

Male. Head, thorax, and general colour of fore-wing bronzy-green; base of fore-wing sulphine yellow (iv), this colour being extended along the costa and over the whole terminal half of wing; area between basal and medial line, except along costa, covered with orange-cinnamon (xxix) scales, heavily irrorated with fuscous-black scales; medial line indicated by fuscous-black scaling; tuft of long white scales below the cell; postmedial consists of black scales, oblique from costa to vein 5, then dentate outwardly between the veins; some triangular fuscous-black scaling beyond it on inner margin, irrorated with orange-cinnamon; cilia showing three parallel shades, first sulphine yellow with black scales at end of veins, second vinaceous-fawn (xl) with some fuscous scales mixed, then the outer scales vinaceous-fawn but lighter at base. Hind-wing uniform fuscous (xlvi), cilia as in fore-wing.

Underside: Both wings fuscous; postmedial line slightly darker, followed by a light vinaceous-fawn colour; cilia as on upperside.

Exp. 30 mm.

Hab. Barisan Range, Western slopes, 2500 ft., S.W. Sumatra, Oct.–Nov. 1921 (*C. F.* and *J. Pratt*).

Unfortunately one specimen only is available, but the structural characters make it easily distinguishable. Type in coll. Janse.

Parastericta, gen. n.

Type: *lanata*, sp. n.

Pl. XXXVII, fig. 11.

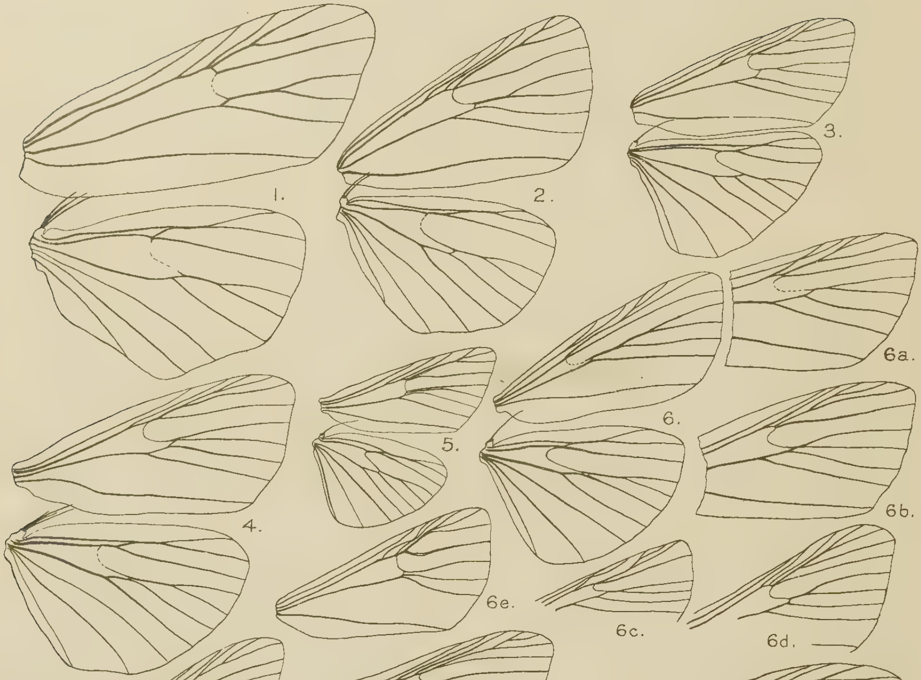
This genus comes fairly close to *Stericta*, but the fore-wing has vein 10 anastomosing with the stalk of 7, 8, 9, forming an areole there, the labial palpi are solid and the maxillary palpi are not covered with long hair but are triangularly scaled. The genitalia are also quite different.

Male, female. Fore-wing with vein 2 from well before the angle; 3, 4, 5 remote and from near lower angle; 6 shortly stalked with 7, 8, 9; 7, 8, 9 stalked; 10 free, then anastomosing for a good distance with the stalk of 7, 8, 9 a little before 7, forming a large areole; 11 approximated to areole, then remote; 12 parallel with 11. Hind-wing with 2, 3, 4, 5 as in fore-wing, only 4, 5 slightly approximated; 6, 7 shortly stalked; 8 touching 7 but still free. Antennae with a process in male, none in female; process cylindrical, roundly pointed and densely covered, especially towards upper half, with spreading scales, at base with many long-stalked scales; shaft fasciculate with long hairs in male, shorter hairs in female. Labial palpi almost as in Pl. XXVIII, fig. 20, but solid and more densely covered with scales, especially towards the apex; maxillary palpi as in Pl. XXVIII, fig. 23. Palpi in female as in male, but less densely scaled.

Hind legs with two pairs of spurs; fore leg with a short process; male and female with a terminal hairy tuft on hind tibiae. Male genitalia: Uncus rather long, with a ridge before distal extremity from which there are a large number of long dense hairs; IXth tergite membranous, with the posterior and anterior edges thinly chitinised; scaphium well developed, long, ending in a curved hook and before the hook somewhat swollen; vinculum narrow and of even width; juxta chitinised; valves rhomboid, thinly covered with fine hairs; penis long, rather slender; aedoeagus terminating in two curved hooks of which one is long and the other shorter.

Parastericta lanata, sp. n.

Male. Ground-colour of head, thorax and fore-wing white; head with warm buff (xv) scales intermixed; antennal process with testaceous scales intermixed; prothorax and scales on legs entirely testaceous (xxviii). Fore-wing with basal third clove-brown (xl) irrorated with black, the outline of the patch sharply defined and oblique from costa to inner margin, leaving a white patch between 1*b* and inner margin; two black spots on costa beyond patch, the last being the beginning of the postmedial line, which is excurved between veins 6 and 3, dentate on the veins and for lower half indicated by clove-brown scaling; a triangular costal clove-brown patch beyond postmedial line, also irrorated with black; terminal area, except actually at termen, clouded with greyish-olive and a similar clouding just beyond basal patch on inner margin; a terminal black line interrupted by white on the veins; cilia warm buff and with some fuscous scaling on end of veins. Hind-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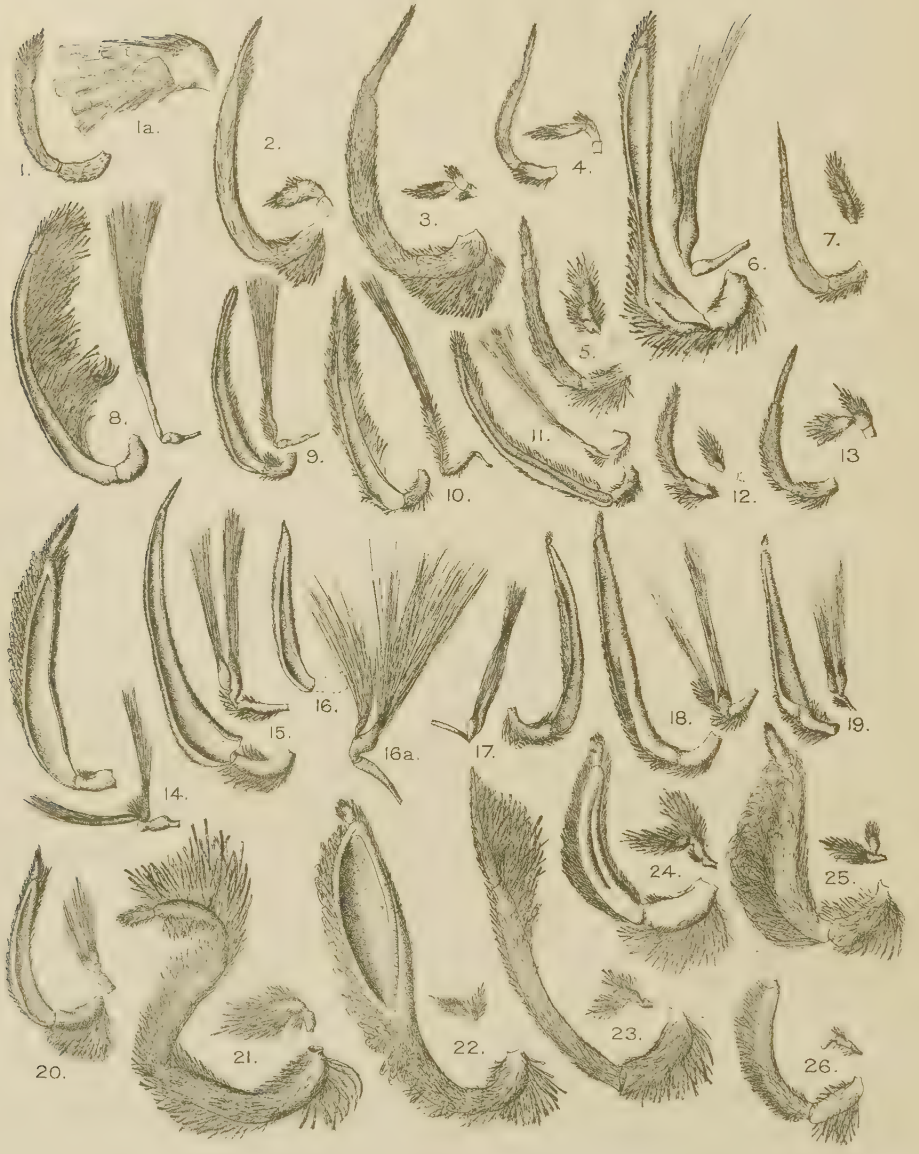
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wing uniformly tinged with deep olive-buff (xl) especially towards termen; postmedial faintly indicated by greyish-olive; terminal line fuscous.

Underside: fore-wing well tinged with greyish-olive and irrorated along upper median with testaceous; hind-wing as on upperside but apical area clouded with greyish-olive and costa broadly irrorated with testaceous.

Female. Like male, but fore-wing with nearly the whole of the terminal half clove-brown from beyond postmedial at costa to lower angle of cell and then straight down to inner margin and densely irrorated with black to postmedial line; postmedial line darker. Hind-wing densely clouded with fuscous (xlvi) but lighter towards base. Underside of both wings clouded with fuscous for greater part of wing and somewhat lighter on the veins of the hind-wing.

I have little doubt that this female belongs to the male, although it is from a different locality.

Exp. in male, 34 mm.; in female, 37 mm.

Male type from W.C. Buru (Miapat, 5000 ft.), April 1922 (*Pratt*); female, Ekeikei, B.C. New Guinea, 1500 ft., March–April 1903 (*A. E. Pratt*).

EXPLANATION OF PLATES XXVII–XXXVII.

PLATE XXVII.

FIG. 1. *Neopaschia flaviciliata*, Janse. ♀, × 8.
2. *Anartula melanophia*, Stgr. ♀, × 3
3. *Oneida luniferella*, Hulst. ♂, × 3.
4. *Tetralopha militella*, Zell. ♀, × 4
5. *Tetralopha atrifascialis*, Hulst. ♂, × 4.
6. *Pococera gibella*, Zell. ♂, × 3.
6*a*. *Pococera gibella*, Zell. ♀, × 3.
6*b*. *Tetralopha militella*, Zell. ♀, × 4.
6*c*. *Tetralopha atromentalis*, Led. ♂, × 4.
6*d*. *Tetralopha fabianalis*, Schaus. ♂, × 4.
6*e*. *Jocara albimedialis*, Hmpsn. ♂, × 3.
7. *Tancoa attenualis*, Hmpsn. ♂, × 4.
8. *Calybitia picata*, Schaus. ♂, × 4.
9. *Micropaschia orthogrammalis*, Hmpsn. ♂, × 8.
10. *Lepidogma rubricalis*, Hmpsn. ♂, × 4.
11. *Jocara trabalis*, Grote. ♂, × 3.
12. *Oedomia hispida*, Dogn. ♂, × 2.
12*a*. *Oedomia hispida*, Dogn. × 8 (costal part of fore-wing).
13. *Termioptycha cyanopa*, Meyr. ♂, × 2.

PLATE XXVIII.

Labial and maxillary palpi.

FIG. 1. *Neopaschia flavociliata*, Janse. Lab. palpus, × 19.
1*a*. *Neopaschia flavociliata*, Janse. Max. palpus, × 110.
2. *Oneida luniferella*, Hulst. Lab. palpus, × 13; max. palpus, × 29.
3. *Tetralopha militella*, Zell. × 19.
4. *Tetralopha atrifascialis*, Hulst. Lab. palpus, × 13, max. palpus, × 29.
5. *Pococera fabianalis*, Schaus. Lab. palpus, × 13; max. palpus, × 29.

Fig. 6. *Jocara albimedialis*, Hmpsn. × 13.
7. *Jocara atromentalis*, Led. Lab. palpus, × 13; max. palpus, × 29.
8. *Tancoa metaxanthalis*, Hmpsn. × 8.
9. *Tancoa attenualis*, Hmpsn. × 8.
10. *Tancoa sinuata*, sp. n. × 8.
11. *Tancoa schausi*, sp. n. × 8.
12. *Micropaschia orthogrammalis*, Hmpsn. × 19.
13. *Lepidogma rubricalis*, Hmpsn. Lab. palpus, × 13; max. palpus, × 29.
14. *Jocara trabalis*, Grote. × 13.
15. *Milgithea argentilinea*, Druce. × 13.
16. *Jocara ferrifusalis*, Hmpsn. Lab. palpus, × 8; max. palpus, × 13.
17. *Oedomia hispida*, Dogn. × 8.
18. *Jocara sara*, Schaus. × 13.
19. *Milgithea rufiapicalis*, Hmpsn. × 8.
20. *Jocara basiochrealis*, Grote. × 13.
21. *Termioptycha conjuncta*, Warr. × 13.
22. *Teliphasa amica*, Butl. × 13.
23. *Termioptycha cyanopa*, Meyr. × 13.
24. *Cecidipta excaecariae*, Berg. × 13.
25. *Locastra crassipennis*, Wlk. × 8.
26. *Chloropaschia thermalis*, Hmpsn. × 13.

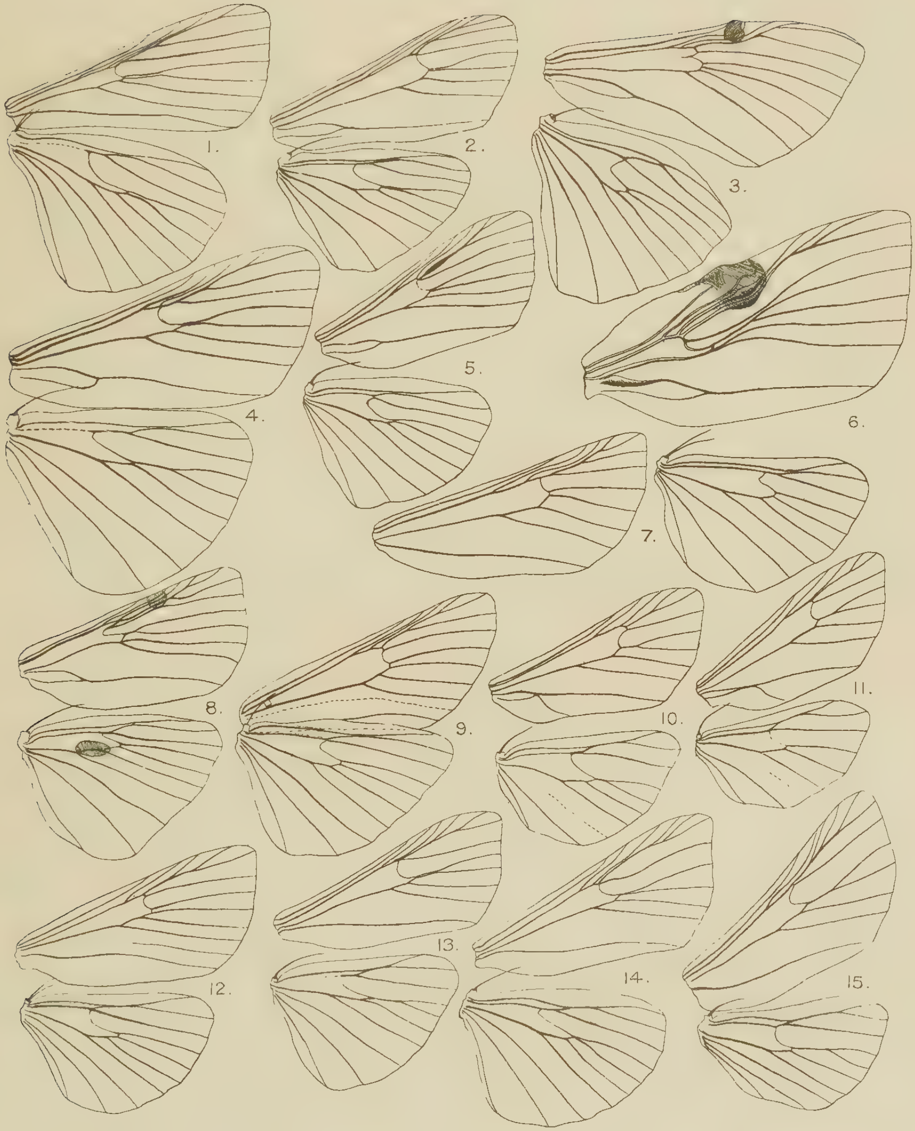
PLATE XXIX.

Fig. 1. *Macalla thyrsisalis*, Wlk. ♀, × 3.
2. *Cecidipta excaecariae*, Berg. ♂, × 2.
3. *Locastra crassipennis*, Wlk. ♂, × 2.
4. *Chloropaschia thermalis*, Hmpsn. ♂, × 4.
5. *Stericta divitalis*, Guen. ♂, × 3.
6. *Orthaga euadrusalis*, Moore. ♂, × 4. Fore-wing only.
7. *Isolopha albicristata*, Warr. ♀, × 2.
8. *Polylophota barbarossa*, Hmpsn. ♂, × 2.
9. *Taeniaphora submarginata*, Kenr. ♂, × 2.
10. *Rhynchopaschia melanolopha*, Hmpsn. ♂, × 4.
11. *Rhynchopaschia reducta*, sp. n. ♂, × 6.
12. *Doddiana callizona*, Low. ♀, × 2.
13. *Paranatula zographica*, Dyar. ♂, × 4.
14. *Milgithea melanoleuca*, Hmpsn. ♂, × 4.
15. *Pocopaschia noctuina*, Schaus. ♂, × 3.

PLATE XXX.

Antennal processes in males.

Fig. 1. *Oneida luniferella*, Hulst. × 13.
2. *Tallula atrifascialis*, Hulst. × 13.
3. *Tancoa attenualis*, Hmpsn. × 13.
4. *Tancoa metaxanthalis*, Hmpsn. × 13.
5. *Tancoa sinuata*, sp. n. × 13.
6. *Tancoa schausi*, sp. n. × 13.
7. *Micropaschia orthogrammalis*, Hmpsn. × 19.
8. *Jocara albimedialis*, Hmpsn. × 13.
9. *Lepidogma rubricalis*, Hmpsn. × 8.
10. *Jocara trabalis*, Grote. × 13.
11. *Jocara basiochrealis*, Grote. × 13.
12. *Jocara sara*, Schaus. × 13.
13. *Oedomia hispida*, Dogn. × 8.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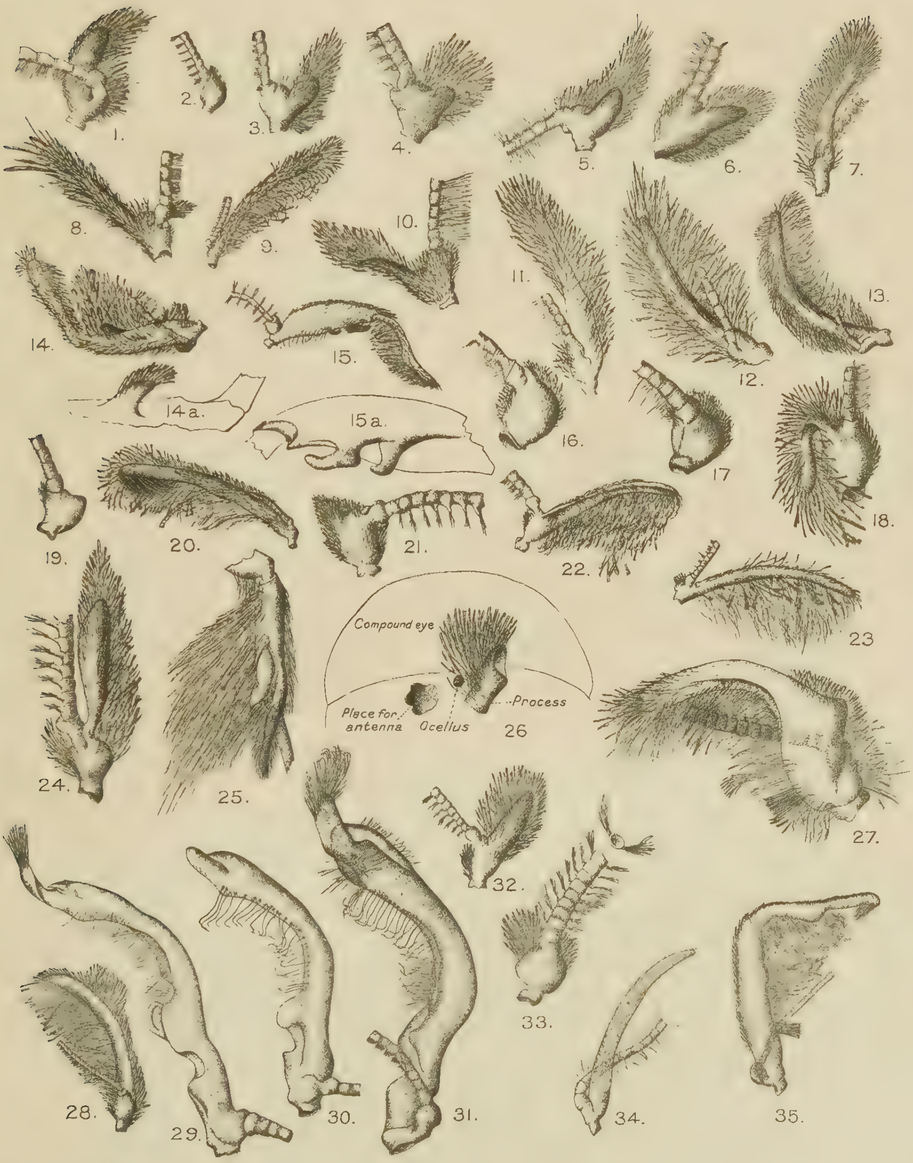
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Compound eye
Place for antenna
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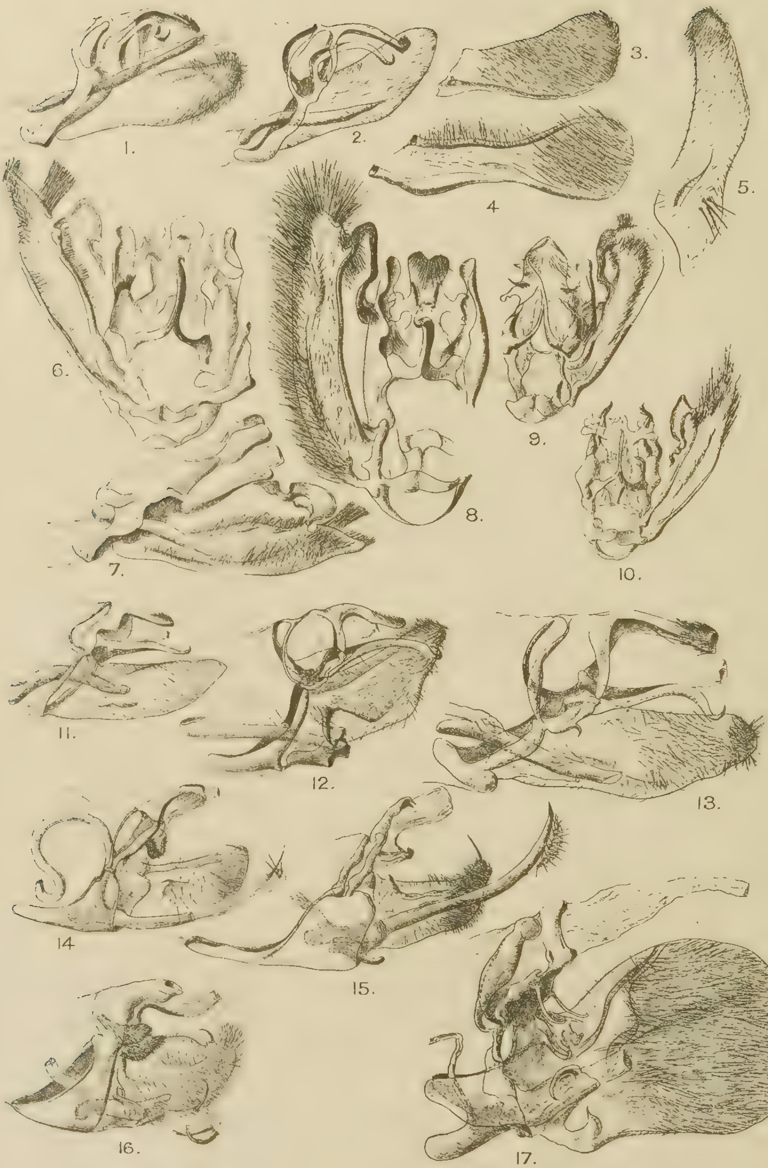
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PLATE XXXII.

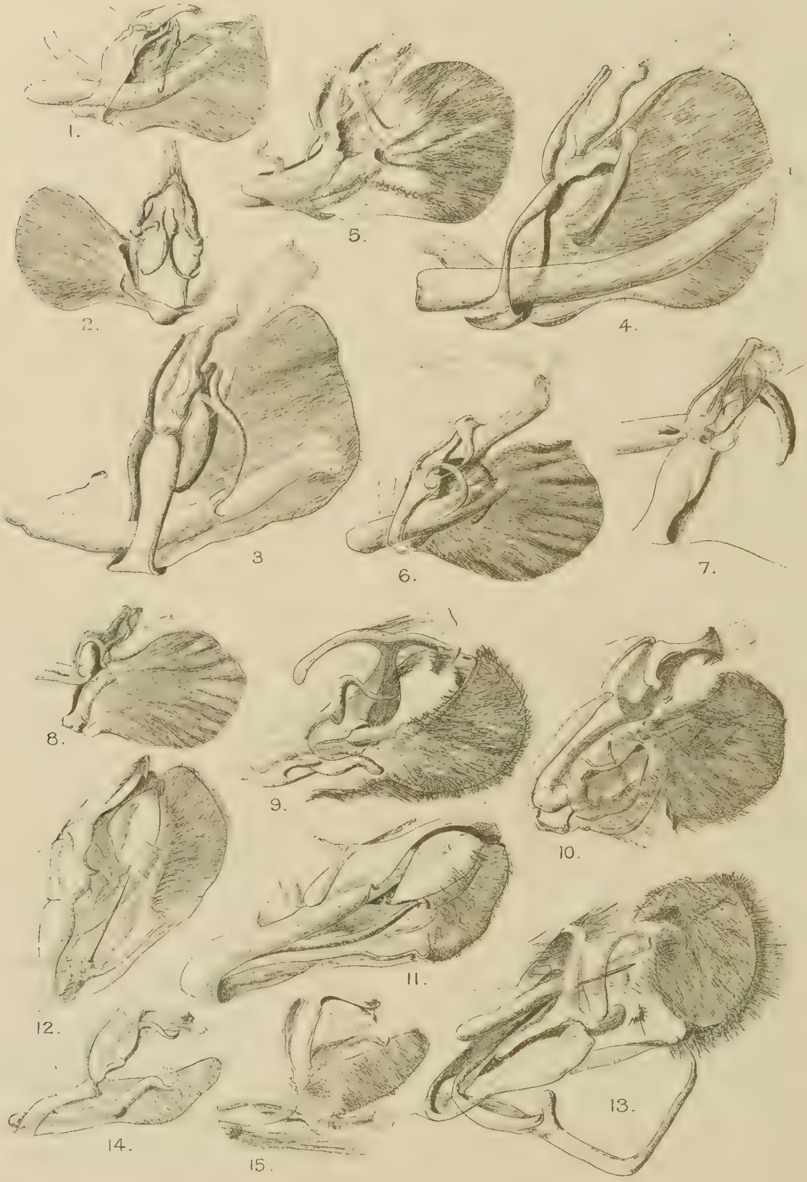
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Fig. 14. *Milgithea rufiapicalis*, Hmpsn. × 8 (seen from inner side).
14*a*. *Milgithea rufiapicalis*, Hmpsn. × 19 (seen from outer side).
15. *Milgithea argentilinea*, Druce. × 8 (seen from inner side).
15*a*. *Milgithea argentilinea*, Druce. × 19 (seen from outer side).
16. *Termioptycha cyanopa*, Meyr. × 13.
17. *Termioptycha conjuncta*, Warr. × 13.
18. *Teliphasa nubilosa*, Moore. × 13.
19. *Lamida moncusalis*, Wlk. × 13.
20. *Epilepia melanosparsalis*, Janse. × 8 (seen from inner side).
21. From unidentified material. × 13.
22. *Lacalma porphyrealis*, Kenr. × 8.
23. *Epipaschia superatalis*, Clem. × 8.
24. *Cecidipta excaecariae*, Berg. × 13.
25. *Locastra crassipennis*, Wlk. × 8. Fore-leg from inner side.
26. *Locastra crassipennis*, Wlk. × 8. Head from above, showing sense-organ.
27. *Locastra crassipennis*, Wlk. × 8. Antennal process.
28. *Stericta divitalis*, Guen. × 8.
29. *Craneophora ficki*, Christ. × 13. } Process of antennae with
30. *Craneophora haraldusalis*, Wlk. × 13. } scales removed but
31. *Craneophora carniola*, Hmpsn. × 13. } with hairs left on.
32. *Polylophota barbarossa*, Hmpsn. × 8.
33. *Taeniaphora submarginata*, Kenr. × 8.
34. *Paranatula zographica*, Dyar. × 13.
35. *Milgithea melanoleuca*, Hmpsn. × 13.

Plate XXXI.

Male genitalia. All lateral preparations have left valve removed.

Fig. 1. *Oneida luniferella*, Hulst. × 13.
2. *Pococera gibella*, Zell. × 19.
3. *Pococera atromentalis*, Led. × 19. Right valve only.
4. *Pococera fabianalis*, Schaus. × 13. Right valve only.
5. *Jocara albimedialis*, Hmpsn. × 19. Left valve only.
6. *Tancoa attenualis*, Hmpsn. × 13. (Dorsi-ventral aspect; penis and right valve omitted.)
7. *Tancoa attenualis*, Hmpsn. × 13. (Lateral view with left valve removed.)
8. *Tancoa schausi*, sp. n. × 13. (Dorsi-ventral view with penis and right valve omitted.)
9. *Tancoa metaxanthalis*, Hmpsn. × 8. (Left valve and penis omitted.)
10. *Tancoa sinuata*, sp. n. × 8. (Left valve and penis omitted.)
11. *Micropaschia orthogrammalis*, Hmpsn. × 19.
12. *Lepidogma rubricalis*, Hmpsn. × 19.
13. *Jocara trabalis*, Grote. × 19.
14. *Termioptycha cyanopa*, Meyr. × 8.
15. *Termioptycha aurantiaca*, sp. n. × 8.
16. *Termioptycha conjuncta*, Warr. × 8.
17. *Teliphasa amica*, Butl. × 8. (From Sumatra.)

Plate XXXII.

Male genitalia. All lateral preparations have left valve removed.

Fig. 1. *Teliphasa picta*, Warr. × 8.
2. *Teliphasa picta*, Warr. × 8. (Dorsi-ventral view with penis and right valve removed.)

Fig. 3. *Teliphasa picta*, Warr. × 13.
4. *Teliphasa picta*, Warr. × 13.
5. *Teliphasa amica*, Butl. × 8. (From China.)
6. *Teliphasa nubilosa*, Moore. × 8.
7. *Teliphasa nubilosa*, Moore. × 8.
8. *Teliphasa nubilosa*, Moore. × 8.
9. *Lamida moncusalis*, Wlk. × 13. (In taking off the valve the sternite and tergite became detached and the whole preparation became tilted.)
10. *Lamida perdentalis*, Kenr. × 8.
11. *Lamida sordidalis*, Hmpsn. × 13.
12. *Lamida buruensis*, sp. n. × 13.
13. *Lamida mediobarbalis*, Hmpsn. × 13.
14. *Epipaschia superatalis*, Clem. × 13.
15. *Lacalma porphyralis*, Kenr. × 8.

Plate XXXIII.

Male genitalia. All lateral views have the left valve removed.

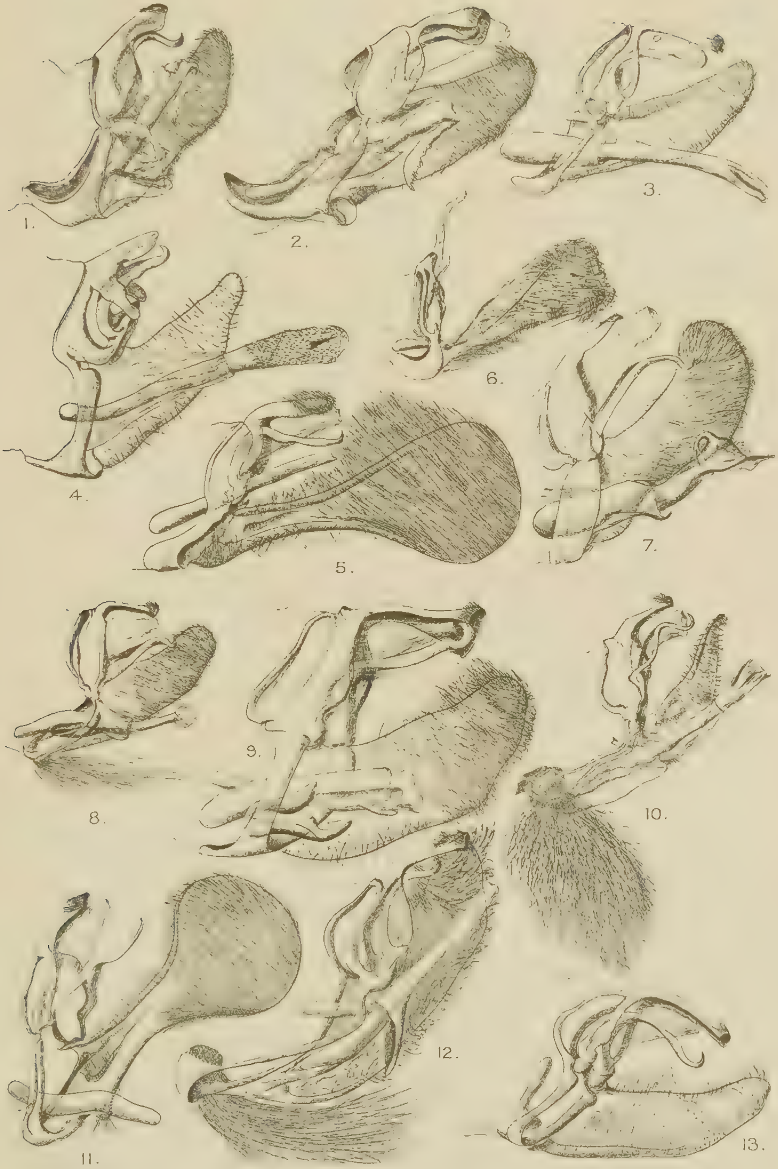
Fig. 1. *Epilepia melanosparsalis*, Janse. × 13.
2. *Epilepia melanobrunnea*, Janse. × 13.
3. *Epilepia* (?) sp. from New Guinea. × 13.
4. *Calomacalla metachryseis*, Hmpsn. × 13.
5. *Chloropaschia granitalis*, Feld. × 13.
6. *Macalla melapastalis*, Hmpsn. × 8.
7. *Macalla* (?*Epipaschia*) *phaeobasalis*, Hmpsn. × 8.
8. *Lacalma porphyrealis*, Kenr. × 8.
9. *Cecidipta excaecariae*, Berg. × 13.
10. *Locastra crassipennis*, Wlk. × 5.
11. *Chloropaschia thermalis*, Hmpsn. × 13.
12. *Orthaga euadrusalis*, Wlk. × 13.
13. *Stericta divitalis*, Guen. × 13.

Plate XXXIV.

Male genitalia, except figures 7, 9, 10, which are palpi.

All lateral views have the left valve removed, and in figures 1 and 2 the penis has been removed.

Fig. 1. *Craneophora ficki*, Christ. × 13.
2. *Craneophora carniola*, Hmpsn. × 13.
3. *Craneophora haraldusalis*, Wlk. × 13.
4. *Polylophota barbarossa*, Hmpsn. × 8.
5. *Taeniaphora submarginata*, Kenr. × 8.
6. *Rhynchopaschia griseata*, Janse. × 30.
7. *Sarama atkinsoni*, Moore. × 20.
8. *Epipaschia zelleri*, Grote. × 13.
9. *Epipaschia zelleri*, Grote. × 13.
10. *Epipaschia zelleri*, Grote. × 8.
11–15. Gen. et sp. incert. Unfortunately only one specimen is so far known to me, and is in such a condition, that I do not think it advisable to use it as the type of a description. The genitalia are extremely peculiar in their modification.
  11. Complete genitalia with the left valve and penis removed.
  12. Right valve seen from the outer side.
  13. Uncus and scaphium seen from the left side.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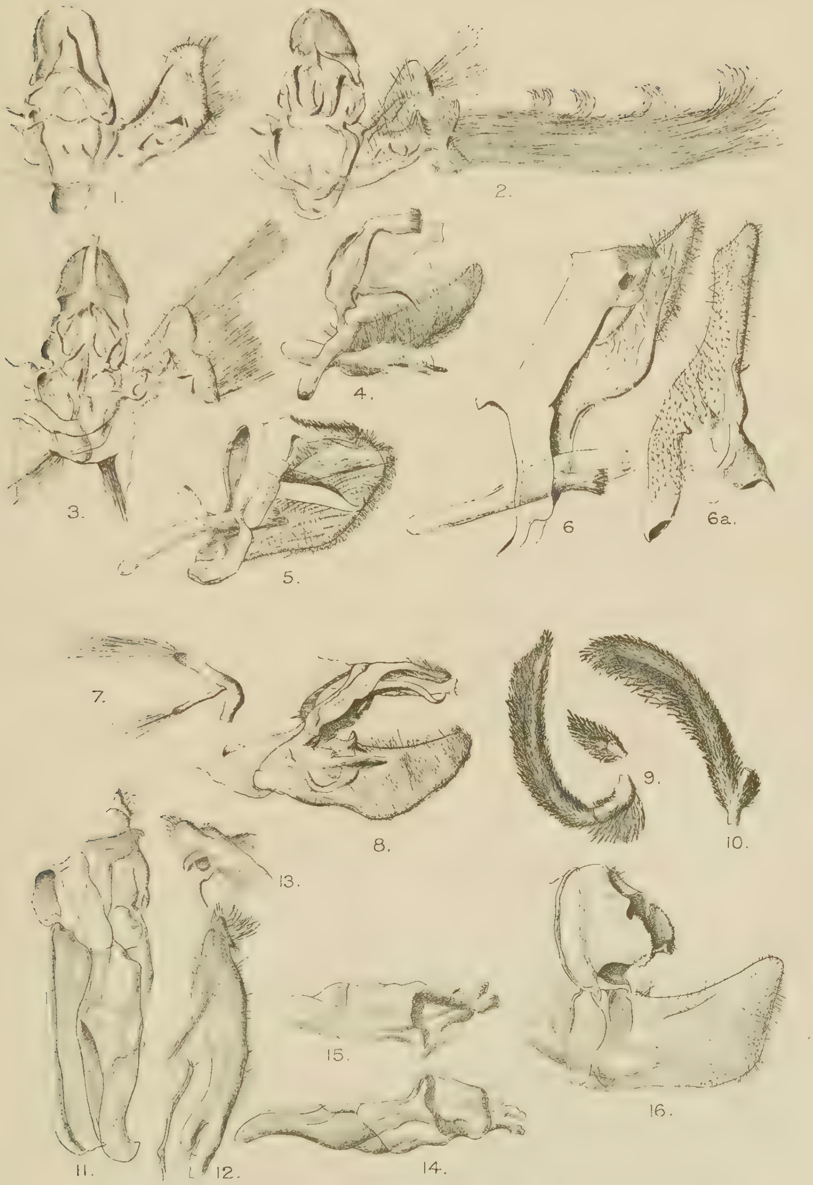
Janse del ad nat
John Bale Sons & Danielsson, Ltd

GENERA OF EPIPASCHIINAE.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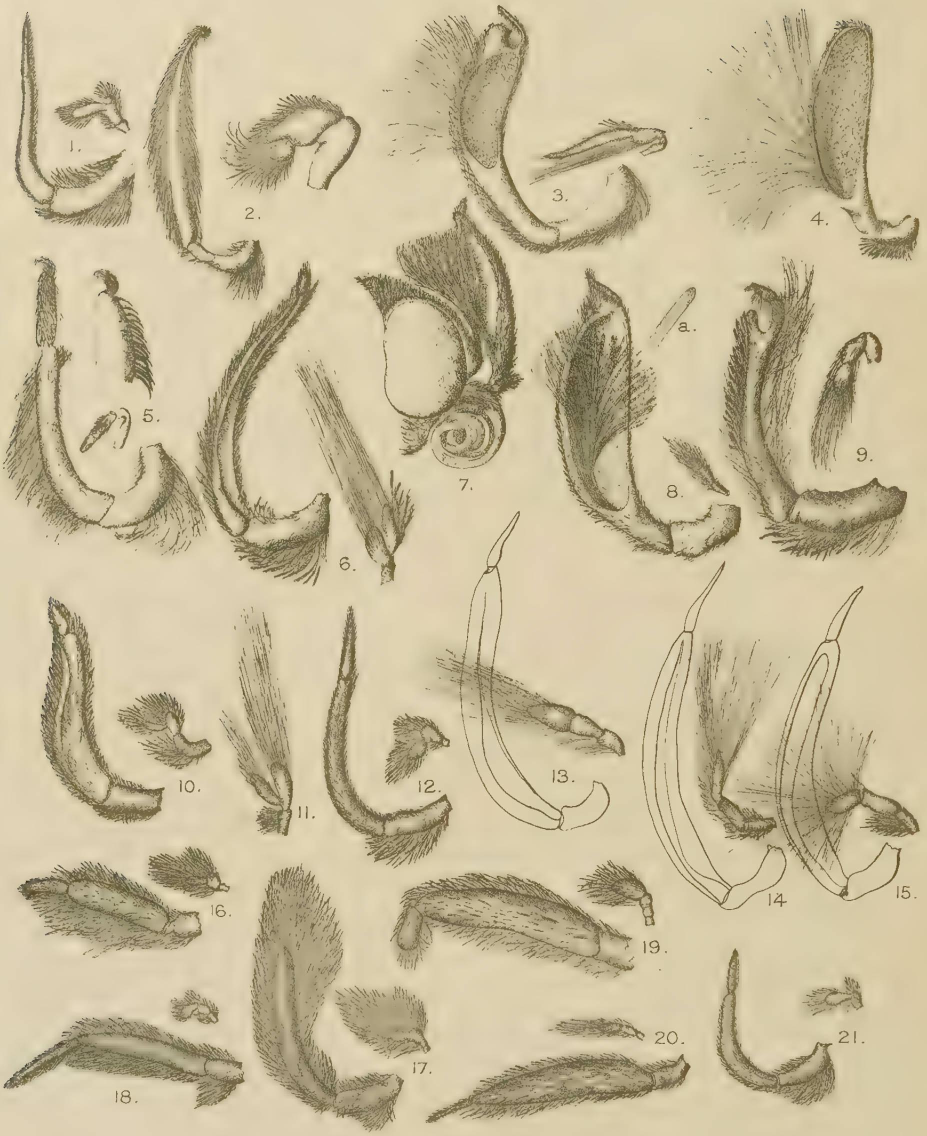
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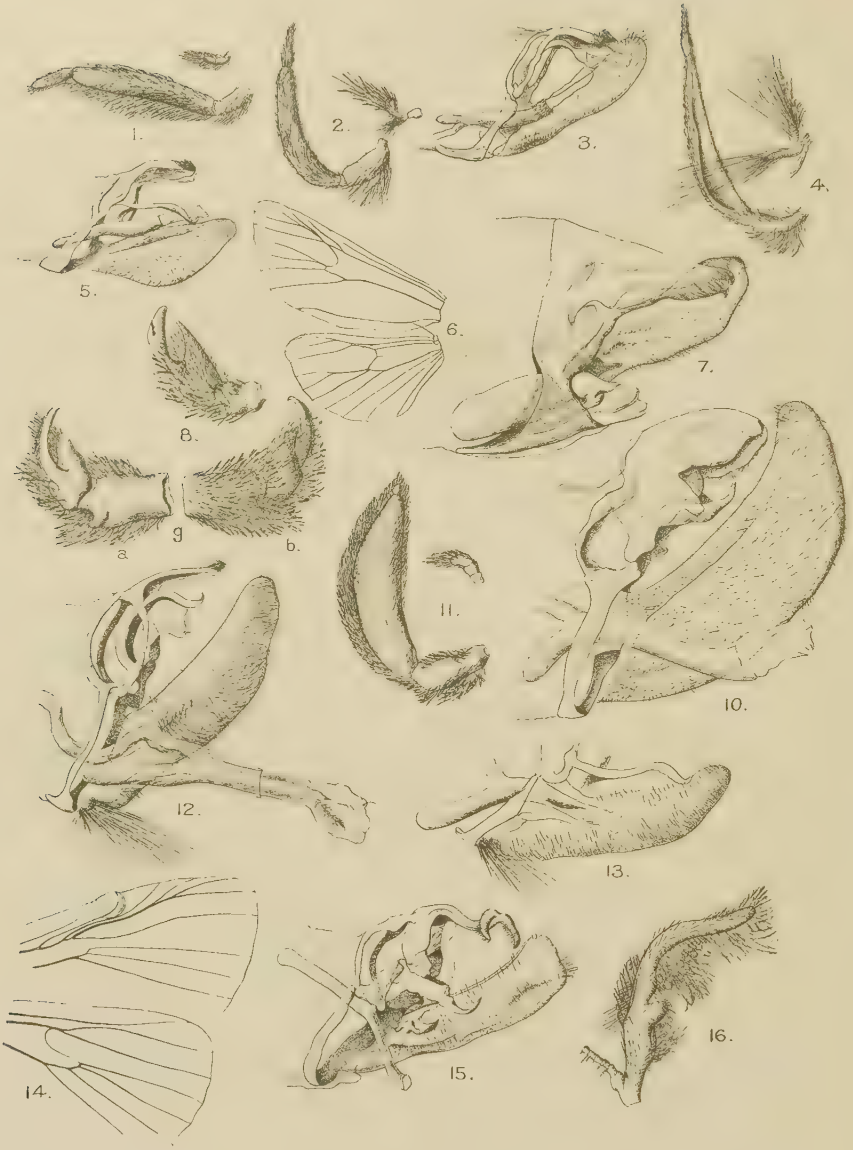
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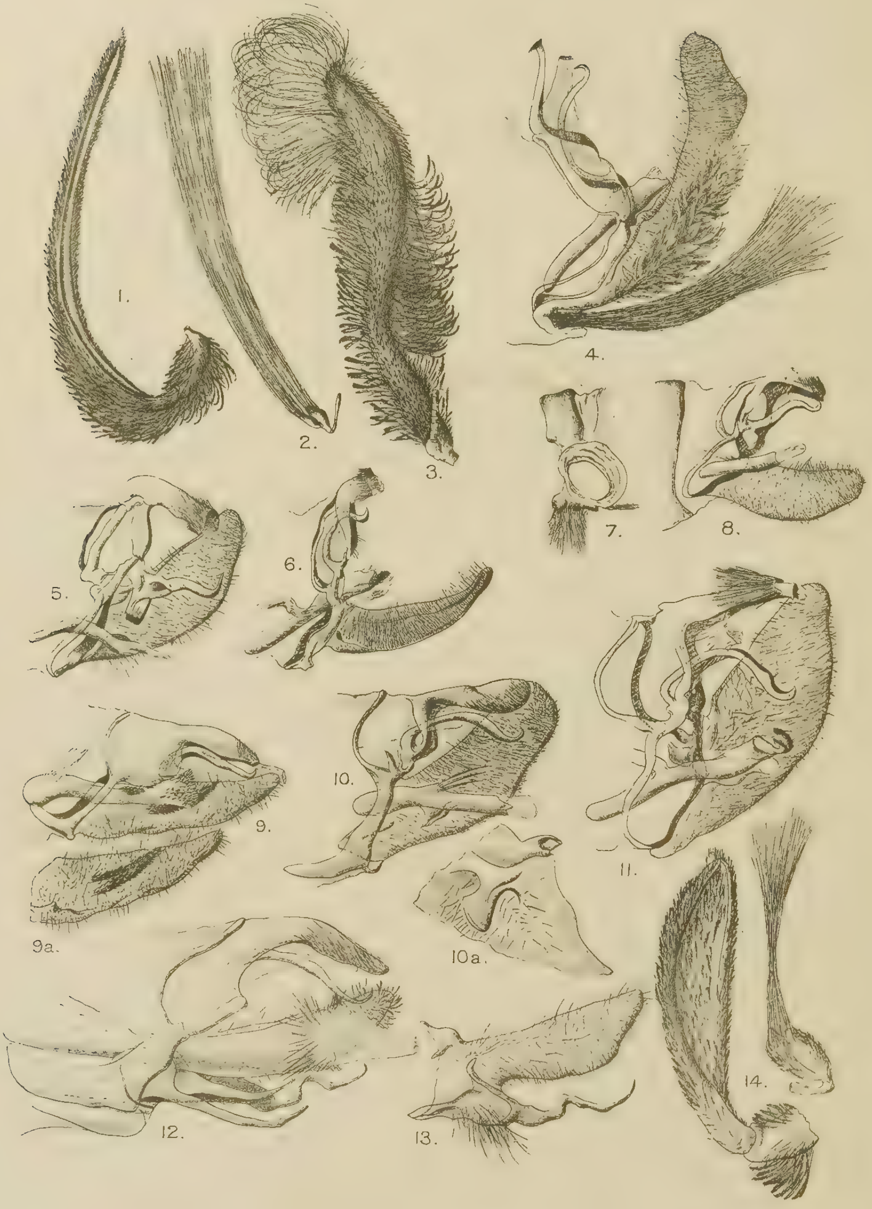
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Janse del. ad nat.

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GENERA OF EPIPASCHIINAE.

FIG. 14. Complete penis seen from the right side.
15. Penis (partly) seen from the left side.
16. Gen. et sp. incert.

PLATE XXXV.

Labial and maxillary palpi.

FIG. 1. *Orthaga euadrusalis*, Wlk. × 13.
2. *Teliphasa nubilosa*, Moore. Lab. palpus, × 13; max. palpus, × 30.
3. *Lamida moncusalis*, Wlk. × 13.
4. *Lamida mediobarbalis*, Hmpsn. × 8.
5. *Lamida perdentalis*, Kenr. Lab. palpus, × 13; max. palpus, × 30.
6. From unidentified material. × 13.
7. *Teliphasa amica*, Butl. Head seen from the side. × 8.
8. *Lamida sordidalis*, Hmpsn. × 13; *a*, × 40.
9. From unidentified material.
10. *Lacalma papuensis*, Warr. × 13.
11. *Lacalma porphyrealis*, Kenr. × 13.
12. *Epipaschia superatalis*, Clem. × 20.
13. *Craneophora ficki*, Christ. × 13.
14. *Craneophora carniola*, Hmpsn. × 13.
15. *Craneophora haraldusalis*, Wlk. × 13.
16. *Isolopha albicristata*, Warr. ♀, × 8.
17. *Polylophota barbarossa*, Hmpsn. × 8.
18. *Taeniaphora submarginata*, Kenr. × 8.
19. *Rhynchopaschia griseata*, Janse. × 20.
20. *Rhynchopaschia reducta*, sp. n. × 20.
21. *Orthaga exvinacea*, Hmpsn. × 13.

PLATE XXXVI.

FIG. 1. *Doddiana callizona*, Low. Palpi, × 8.
2. *Paranatula zographica*, Dyar. Palpi, × 20.
3. *Paranatula zographica*, Dyar. Genitalia, × 20.
4. *Milgithea melanoleuca*, Hmpsn. Palpi, × 13.
5. *Milgithea melanoleuca*, Hmpsn. Genitalia, × 13.
6. *Pocopaschia accelerans*, Dyar. Wings, × 3.
7. *Pocopaschia noctuina*, Schaus. Genitalia, × 13.
8. *Pocopaschia accelerans*, Dyar. Palpus, × 20.
9. *Pocopaschia noctuina*, Schaus. Palpus, *a* from inside; *b* from outside, × 20.
10. *Coenodomus hockingii*, Wlshm. Genitalia, × 13.
11. *Coenodomus hockingii*, Wlshm. Palpi from inner side, × 13.
12. *Orthaga basalis*, Moore. Genitalia, × 13.
13. *Orthaga exvinacea*, Hmpsn. Genitalia (partly drawn), × 13.
14. *Orthaga exvinacea*, Hmpsn. Male, wing (partly drawn), × 4.
15. *Sarama atkinsoni*, Moore. Male, Genitalia, × 13.
16. *Sarama atkinsoni*, Moore. Male, antennae, × 8.

PLATE XXXVII.

FIG. 1. *Plumiphora pratti*, sp. n. Labial palpus, × 8.
2. *Plumiphora pratti*, sp. n. Maxillary palpus, × 8.
3. *Plumiphora pratti*, sp. n. Antennal process, × 8.
4. *Orthaga jucundalis*, Wlk. Genitalia, × 20.
5. *Titanoceros cataxantha*, Meyr. Genitalia, × 20

FIG. 6. *Polylophota senilis*, sp. n. Genitalia, × 8.
7. *Jocara conspicualis*, Led. Base of abdomen, × 13.
8. *Jocara conspicualis*, Led. Genitalia, × 13.
9. Gen. et sp. incert. Genitalia, *a*, valve seen from the outside, × 20.
10. *Epilepia simulans*, sp. n. Genitalia, × 13; *a* left valve seen from the inside, × 13.
11. *Parastericta lanata*, sp. n. Genitalia, × 13.
12. *Macalla thyrsisalis*, Wlk. Genitalia, × 13.
13. *Macalla thyrsisalis*, Wlk. Left valve seen from the outside, × 13.
14. *Macalla thyrsisalis*, Wlk. Male. Palpi, × 13.

NEW MATERIAL REGARDING THE DATES OF THE PLATES OF THE *PAPILIONES* IN JACOB HÜBNER'S "SAMMLUNG EUROPÄISCHER SCHMETTERLINGE," WITH NOTES ON THE SYNONYMY AND TYPE LOCALITIES OF CERTAIN SPECIES DESCRIBED THEREIN

By Captain A. F. Hemming, C.B.E.

[Read 3rd June, 1931.]

1. The uncertainty regarding the dates of the plates of Hübner's *Sammlung europäischer Schmetterlinge* has long been a source of great difficulty to systematists, as in many cases questions of priority depend on the dates assigned to them. In the course of some other work, I have recently collected a number of references to the later plates of Hübner's Volume I (*Papiliones*) in contemporary entomological literature. These references are of value as affording the strongest presumptive evidence that the plates in question were issued *not later* than the dates of the works in which they are quoted. Another line of evidence is afforded by four instances in which the figures in Hübner's plates are mere copies of figures from other works of known date. Data of this kind show that the plates in question were issued *not earlier* than the known dates of the works from which they were copied.

2. The dates currently assigned (*e.g.* in Sherborn, *Index Animalium*) to the plates in Hübner's *Sammlung* are those propounded after long study by Fernald (1905). That author gives his reasons for thinking that the plates of the *Papiliones* may be assigned to twelve different periods, between the years 1799 and 1841. It is necessary to give the following short summary of his argument in order to examine (*a*) how far his conclusions may be logically deduced from the data at his disposal and (*b*) in what directions they require modification in the light of the material that has since been collected :—

(*a*) Volume II of Illiger's edition of Schiffermuller's *Syst. Verz. Wien. Gegend* contains references to 8 plates of which the latest is plate 88. From the evidence afforded by the preface to Volume I (which states that Volume II was then in the press) Fernald concludes that all works referred to in Volume II must have been published not later than the end of 1799.

(*b*) Part 1 (dated July 1803) of Haworth's *Lepidoptera Britannica* contains references to plates 1–96.

(*c*) Hoffmansegg reviews plates 1–114 in Illiger's Magazin, Volume III, issued in 1804.

(*d*) Hübner's text of the *Sammlung* issued in 1805 contains references to plates 1–124.

(*e*) Volume I (2) of Ochsenheimer's *Schmett. Europa* published in 1808 gives references as far as plate 128.

(*f*) Volume IV of the above work by Ochsenheimer published in 1816 gives references up to plate 147.

(*g*) In the preface (dated January 1818) to his *Verzeichniss der europäischen Schmetterlinge*, Charpentier states that he possesses plates 1–150. Fernald, therefore, concludes that all the above plates were published before the end of 1817.

TRANS. ENT. SOC. LOND. 79. PART III. (DEC. 1931.)

(*h*) Hübner's *Systematisch-alphabetisches Verzeichniss* (the preface to which is dated September 22nd, 1822) contains references to plates 1–154.

(*i*) Hübner's Prospectus No. V, dated December 22nd, 1823, states that plates 1–161 were available.

(*j*) In Volume I (p. 101) of Silbermann's *Revue Entomologique* (the preface to this part of which is dated January 1833) there is a notice of the parts of Hübner's work for sale by Geyer. This notice refers to plates 1–195.

(*k*) Hübner's Prospectus No. VI, dated January 1st, 1834, gives 196 plates as then available.

(*l*) Fernald assumes (without giving his reasons) that the last plate was issued in 1841, and therefore that plates 197–207 were issued between 1834 and 1841.

3. On the basis of the foregoing data Fernald drew up the following table :—

Plates 1–88	1799.
,, 89–96	1802.
,, 97–114	1804.
,, 115–124	1805.
,, 125–128	1808.
,, 129–147	1808–1816.
,, 148–150	1817.
,, 151–154	1818–1822.
,, 155–161	1823.
,, 162–195	1823–1833.
,, 196	1834.
,, 197–207	1834–1841.

4. Before discussing the new material available the following observations are offered on Fernald's conclusions :—

(1) As regards conclusion (*b*) above, the assignment in the final table of the year 1802 for plates 89–96 is inconsistent with the evidence afforded by Haworth's work, which is dated July 1803. Possibly 1802 in the table is a misprint for 1803. Further, there is nothing to show that these plates were not published any time after the end of 1799 up to 1803. The possible range of date for these plates is, therefore, 1800–1803.

(2) Similarly, as regards plates 97–114, there is nothing to show that they were not published in 1803. Hoffmansegg's article only shows that they were, in fact, published at the time that he wrote the review published in 1804.

(3) For similar reasons, plates 115–124 may have been published in 1804 and plates 125–128 at any time between 1805 and 1808.

(4) For plates 129–147, Fernald gave the date 1808–1816, though in the cases cited above he had omitted to give the corresponding possible range of date, giving only the latest possible date.

(5) Since the preface to Charpentier's work is dated as early in 1818 as January, I agree that there is every justification for assuming that all the plates referred to therein (plates 1–150) were published by the end of the previous year. There remains the possibility that they might have been published in 1816.

(6) Fernald's treatment of the dates of plates 151–154 is consistent with

the course he adopted with regard to plates 129–147 and enhances the inconsistency (referred to in (4) above) of his treatment of plates 125–128.

(7) Plates 155–161 (see conclusion (*i*) above) were not necessarily published in 1823. They may have been published at any time between September 22nd, 1822, and December 22nd, 1823.

(8) As regards conclusion (*j*) above, the logical course seems to be to regard all the plates (1–195) referred to in Silbermann's *Revue* as having been published by the end of 1832, in view of the fact that the preface to the *Revue* is dated January 1833. Fernald, however, adopted the year 1834, although he followed the opposite course (see conclusion (*g*) above) when considering the exactly similar case of Charpentier's *Verzeichniss.*

(9) The same inconsistency is seen in his treatment of the date of plate 196 (see conclusion (*k*) above). Here the work in which it is quoted (Hübner's Prospectus No. VI) is actually dated January 1st, 1834, and the plates referred to therein must have been published by the end of 1833.

5. In the following table is given in summarised form the information collected regarding plates 162 onwards quoted in more or less contemporary literature and the conclusions that can be drawn therefrom.

Plate.	Fig.	Name.	Work in which quoted and date.	Conclusion regarding date of publication of plate quoted.
163	812–3	*astasia*	Frr., 1828, *Beitr. Gesch. europ. Schmett.* 1 (6): 97	1828 or earlier
164	814–7	*marmorae*	*Id.*, 1829, *Ibid.*, 2 (12): 63	1829 or earlier
166	822–5	*cyrene*	*Id.*, 1829, *Ibid.*, 2 (12): 70	
167	828–9	*dolus*	*Id.*, 1829, *Ibid.*, 3 (17): 7	
170	842–4	*paramegaera*	*Id.*, 1829, *Ibid.*, 2 (12): 64	
172	851–4	*sebrus*	Boisduval, 7 July 1832, *Icones hist. lépidopt. Europe* 1 (5 and 6): 72	Before July 1832
173	855–8	*epistygne*	Frr., 1832, *Neuere Beitr. Schmett.* 1 (8): 97	1832 or earlier
180	890–1	*cerisyi*	Frr., 1830, *Beitr. Gesch. europ. Schmett.* 3 (22): 109	1830 or earlier
181	892–5	*bonellii*	Frr., 1832, *Neuere Beitr. Schmett.* 1 (13): 137	1832 or earlier
185	910–3	*cassandra*	Frr., 1830, *Beitr. Gesch. europ. Schmett.* 3 (22): 110	1830 or earlier
187	918–21	*proto*	Charpentier, 1830, *in* Esper, Die Schmett Suppl. 1–4 Theils: 32	1830 or earlier
199	984–7	*neoridas*	*Id.*, 1836, *Neuere Beitr. Schmett.* 2 (32): 158	1836 or earlier
203	1006–9	*eupheno* var. *douei*	Keferstein, Nov. 1840, *Ent. Z. Stettin,* 1 (11): 172	November 1840 or earlier

6. There remain the data supplied by (*a*) cases in which Hübner's plates are mere copies of plates in other works, and (*b*) cases where a guide to the date of Hübner's plates is afforded by the fact that they contain figures (and names) of species described by other authors during the period under review. The data collected under these headings and the conclusions that may be drawn therefrom may be summarised as follows :—

Plate 202, fig. 1002–3 *ceto.*

These figures are copied from the figures of *phorcys* given by Frr., 1836, *Neuere Beitr. Schmett.*, **3** (33) : 4, plate 193, fig. 2 ♂. Hübner's plate must, therefore, have been published in 1836 or later.

Plate 203, fig. 1006–9 *douei.*

This name was first used by Boisduval in April 1836 in Roret's *Suite à Buffon Lépid.*, **1** : 563. This plate must, therefore, have been engraved after April 1836.

Plate 204, fig. 1010–11 *damone.*

These figures (see H.-S., *Bearb. Schmett. Europ.*, **1** : 101) are copies of those given by Feisthamel in *Ann. Soc. ent. France*, **6** (3) : 301, plate 12, fig. 1. Part 3 of this volume of the *Annales* was issued in 1837 (after September). Hübner's plate 204 must, therefore, be later than September 1837, and plate 203 cannot be later than that date.

Plate 205, fig. 1014–15 *selenis.*

These figures (see H.-S., *l.c.* **1** : 33) are copies of those given by Lefebvre in *Ann. Soc. ent. France*, **6** (1) : 15, plate 1, fig. 3, 4 ♂. This part of Volume 6 was issued in 1837 at some date after the end of March.

Plate 206, fig. 1023–4 *rhodopensis.*

These figures (see H.-S., *l.c.* **1** : 25) are copies of the figure given by Freyer in his *Neuere Beitr. Schmett.*, **3** (33) : 3, plate 193, fig. 1 ♂, published in 1836.

7. Hübner's Prospectus No. V shows that plates 1–161 had been published by December 22nd, 1823, and it may, therefore, certainly be assumed that plate 162 and following plates were not published earlier than 1824. With this consideration in mind, the following conclusions may be drawn from the new information summarised in the preceding paragraphs :—

Plates 162–163	1824–1828.
,, 164–170	1824–1829.
,, 171–187	1824–1830.
,, 188–199	1824–1836.
,, 200–203	1836–1837.
,, 204–207	1837–1841 (when the work was finished).

8. This information can be made much more precise by paying regard to the information to be drawn from Silbermann's *Revue* regarding the date of plate 195 (see paragraph 4 (8) above on Fernald's conclusions) and from Hübner's Prospectus No. VI (see paragraph 4 (9) above). When account is taken of these factors, the revised dates for plates 162–207 are, on the basis of all information so far referred to, as follows :—

Plates 162–163	1824–1828.
,, 164–170	1824–1829.
,, 171–187	1824–1830.
,, 188–195	1824–1832.
,, 196	1833.
,, 197–199	1834–1836.
,, 200–203	1836–1837.
,, 204–207	1837–1841.

9. There are, however, two other possible sources of information, viz. the date of Hübner's death and the date of the beginning of Geyer's continuation, to which no attention has ever been paid. Hübner died at Augsburg on September 13th, 1826. Obviously, it would be of the first importance if it were possible to ascertain (*a*) how many plates were published by Hübner before his death and (*b*) when Geyer issued the first plate of his continuation. Fortunately, this information is available in an article by Herrich-Schaffer (1869), in which he gives in tabular form a statement regarding the whole of the dates of the *Sammlung* which is based on information furnished by Geyer. In this table it is highly significant that in the following series of plates *Papilio*, *Sphinx*, *Bombyx*, *Noctua*, *Geometra*, *Pyralis*, *Tortrix* and *Tinea* (*i.e.* in every set of plates except *Alucita* which was completed in 1823,) the last block of plates is given as having been published in the period 1827–1841. Having regard to the fact that this is Geyer's own list, there is no doubt whatever that the plates given as having been published in that period (which opens three months after Hübner's death) are the plates for which Geyer is solely responsible. In the case of the *Papiliones* the plates given for the period 1827–41 are plates 182–207. It may further be assumed with confidence that plate 181 (the last of Hübner's own plates) was published not later than September 1826, the date when Hübner died. It will be seen at once from the following table what an important effect this information has on previous ideas regarding the dates of plates 162–195, viz. :—

Plates 162–181	1824–September 1826.
,, 182–187	1827–1830.
,, 188–195	1827–1832.

10. It is now possible to summarise the conclusions that I have reached in the light of the material discussed in this paper; but before doing so, it is important to observe that from the point of view of deciding the date to be assigned to a particular plate (or a particular work) the governing date is, in the view of the International Commission on Zoological Nomenclature, the *latest* date at which a plate (or work) containing a new name may have been published. To take an imaginary case, if a species is described under name A in a work for which the best available date is (say) 1808–1818, and under name B in a work published in 1817, name B being published in 1817 would take priority of name A, since the work in which the latter was published, having been published in the period 1808–1818, would only take status for purposes of priority as from 1818. In the following table I give the plates of the *Papiliones* (with their corresponding figures), my conclusions regarding their date of publication, and the date to be assigned to them for purposes of priority in relation to other works. Finally, I have added a column indicating which conclusions are in accordance with those reached by Fernald and which are my own.

Plates.	Figures.	Dates so far as can be ascertained.	Dates for purposes of priority.	Authority for date assigned.
1–88	1–446	1799	1799	Fernald
89–96	447–490	1799–1803	1803	see para. 4 (1)
97–114	491–588	1803–1804	1804	see para. 4 (2)
115–124	589–636	1804–1805	1805	see para. 4 (3)
125–128	637–652	1805–1808	1808	see para. 4 (3)
129–147	653–741	1808–1816	1816	Fernald
148–150	742–756	1816–1817	1817	see para. 4 (5)
151–154	757–774	Jan. 1818–Sept. 1822	1822	Fernald and see para. 4 (6)
155–161	775–806	Sept. 1822–Dec. 1823	1823	see para. 4 (7)
162–181	807–895	Jan. 1824–Sept. 1826	1826	see paragraphs 7 and 9
Geyer's Continuation.				
182–187	896–921	Jan. 1827–1830	1830	see paragraphs 7 and 9
188–195	922–968	Jan. 1827–Dec. 1832	1832	see paragraphs 4 (8), 8 and 9
196	969–974	1833	1833	see para. 4 (9)
197–199	975–987	Jan. 1834–1836	1836	see para. 8
200–203	988–1009	1836–1837 (after April)	1837	see para. 7 and 8
204–207	1010–1029	1837 (after Sept.)–1841	1841	see para. 7 and 8

The following notes indicate the effect on synonymy of the changes indicated above in the dates to be assigned to Hübner's plates. As Hübner published no text for these plates, I have added such particulars as I have been able to collect regarding the type localities of species first described in this part of Hübner's work.

PAPILIONIDAE.

1. **Zerynthia hypsipyle cassandra,** Geyer.

Papilio cassandra, Geyer. Plate 185, figs. 910, 911 ♂, 912, 913 ♀ [1827–1830].

This is the first publication of this subspecies of *Zerynthia hypsipyle*, Schulze (1776) [=*polyxena*, Schiff., 1775, invalid because a primary homonym]. Freyer, who was the first author subsequently to write of *cassandra* (1831, *Neuere Beitr. Schmett.*, **1** (2) : 13), says that it is found in the Greek Islands and in Corsica. Boisduval (1832) says that it occurs at Hyères in Provence. Duponchel (1834) gives, as localities, the Morea and Italy. Geyer's figures correspond well with specimens found in Central Italy to which the name *cassandra* is often applied (*e.g.* Verity and Querci, 1924, *List of Grypocera and Rhopalocera Peninsula Italy* : 22). In the absence of evidence to the contrary, it appears reasonable to use this name in this way, in view, especially, of the fact that Freyer (1831) himself says that *cassandra* is the same as his *demnosia* and that *demnosia*, originally a ms. name of Dahl's, was given by him to specimens taken at Florence (cf. H.-S., 1845, *Syst. Bearb. Schmett. Europ.*, 1 : 142).

PIERIDAE.

2. **Pieris narcaea,** Frr.

Papilio ergane, Geyer. Plate 184, figs. 904, 905 ♂, 906, 907 ♀ [1827–1830].

As the date of this plate is 1827–1830 (1830 for purposes of priority), Geyer's name *ergane* falls as a synonym to *narcaea,* Freyer, which was published in 1828

(*Beitr. Gesch. europ. Schmett.*, **1** (8) : 147). Freyer says that *narcaea* occurs in Dalmatia and also near Florence. Duponchel (1834 in Godart, *H.N. Lépidopt. France*, Suppl. **1** (Diurnes) : 290), writing of the species under the name *ergane*, says that it was discovered by Dahl at Ragusa. This should therefore be regarded as the type locality. It is probable that as in the case of *herta* (cf. *postea*) Geyer received his specimens from Dahl.

3. **Euchloe ausonia,** Hb.

Papilio marchandae, Geyer. Plate 188, figs. 926, 927 ♂, 928 ♀ [1827–1832].

This is the same as the species usually known as *Euchloe simplonia*, Boisd. (1832), though in fact that name was first published in 1829 by Freyer (*Beitr. Gesch. europ. Schmett.*, **2** (13) : 87). Of the two names, *simplonia*, published in 1829, would take precedence of *marchandae*, published in the period 1827–32, if both, as Lord Rothschild (1914) has pointed out, were not identical with, and therefore fall to, *ausonia*, Hb. (plate 113, figs. 582, 583 ♀ published in 1804). The type locality of the latter is given as Italy, *i.e.* presumably some place on the Italian side of the Alps. If, as I have no doubt, *ausonia*, Hb. [= *simplonia*, Frr. & Boisd.], is a separate species distinct from the species formerly known as *belia*, Cr., and more recently (wrongly) as *ausonia*, Hb., the latter should be known by the specific name *crameri*, Butl. (1869). The latter was proposed by Butler as a nom. nov. pro *belia*, Linn., Cramer *nec* Linn., and its type locality is Smyrna, the locality of Cramer's specimen.

LYCAENIDAE.

4. **Cupido sebrus,** Hb.

Papilio sebrus, Hb. Plate 172, figs. 851, 854 ♂ [1824–1826].

The determination of the period 1824–1826 for this plate at last definitely establishes the priority of *sebrus*, Hb., over *osiris*, Meigen (1829), for this species of *Cupido*. Boisduval (1832, *Ic. Hist. Lépidopt. Europe*, **1** (5 and 6) : 72) states that this species was discovered at St. Maximin in Provence by the Count de Saporta, who is known (from the data available in regard to *Uranops escheri*, Hb.) to have corresponded with Hübner through Escher of Zurich. This locality may therefore be taken as the type locality of *sebrus*. Hübner's figures (figs. 852, 853) of the ♀ are not referable to *sebrus*, as they represent a small ♀ of *Cyaniris semiargus*, Rott. (1775).

5. **Aricia nicias,** Meigen.

Papilio donzelii, Boisduval. Geyer, Plate 193, figs. 955, 956 ♂, 957 ♀ [1827–1832].

This name was published in 1832 both by Boisduval (livraison 5 and 6 appeared on July 7th) and by Duponchel. The former says that he discovered it near Briançon in 1825, and that he dedicated it to his friend Monsieur Donzel of Lyon. The name is therefore clearly Boisduval's. It is probable, however, that it had been in circulation for some time as a ms. name, as otherwise it is not possible to explain how Duponchel, who was not in communication with Boisduval, could have published the species almost simultaneously under the same name. For the reasons explained in the earlier part of this paper, I date this plate (plate 193) as having been published by Geyer in the period 1827–1832. The probability is that it appeared before either Boisduval's or Duponchel's.

The point is, however, not material, as in either case the name *donzelii* falls as a synonym to *nicias*, Meigen (1829).

6. **Uranops escheri,** Hb.

Papilio escheri, Hb. Plate 175, figs. 867, 868 ♀ [1824–1826].

This species was first figured by Hübner in 1823 on plate 160. He gives no text, but fortunately it is possible to determine the type locality exactly from a note given by Duponchel (1832 in Godart, *H.N. Lépidopt. France,* Suppl. **1** (Diurnes) : 71), who states that this species was discovered at La Sainte Baume in the Département du Var by the Count de Saporta, who gave it the ms. name *escheri* and sent specimens to Escher of Zurich, by whom they were communicated to Hübner for figuring. La Sainte Baume is thus without doubt the type locality of *escheri.*

7. **Agrodiaetus admetus ripartii,** Frr.

Papilio ripertii, Geyer. Plate 194, figs. 958, 959 ♂, 960 ♀ [1827–1832].

There has been a good deal of confusion in regard to this subspecies, the earliest references to which are :—

Lycaena ripartii, Frr., 1830, *Beitr. Gesch. europ. Schmett.*, **3** (23) : 128.
Argus rippertii, Boisd., 1832 (July 7), *Ic. hist. Lépidopt. Europe*, **1** (5 & 6) : 68.
Polyommatus rippertii, Boisd., Dup. 1832 in Godart, *H.N. Lépid. France*, Suppl. **1** (Diurnes) : 61.
Papilio ripertii, Geyer, 1827–1832 in Hübner, *Samml. Europ. Schmett.*, **1**, plate 194.
Lycaena rippertii, Treitschke, 1834 in Ochsenheimer, *Schmett. Europa*, **10** (1): 62.

Boisduval states that this insect was discovered at Digne in 1829 by Monsieur Rippert de Beaugency, after whom he named it. This is confirmed by Duponchel and Treitschke. As in the case of *donzelii* referred to above, it may be assumed that this insect was in circulation under the ms. name *rippertii* before it was published by Boisduval in 1832, and that it was in this way that Freyer received the specimens which he described and figured in 1830 (*i.e.* two years before the description was published by Boisduval) under the name *ripartii*, which is obviously a corruption of *rippertii.* Freyer says that his specimen came from Spain, but in view of the fact that the name that he applied to his insect is that of its discoverer at Digne, it cannot be doubted that Freyer's locality is a mistake (there are other similar mistakes in his work) and that his specimens actually came from Digne.

8. **Glaucopsyche melanops,** Boisd.

Papilio saportae, Geyer. Plate 188, figs. 922, 923 ♂, 924, 925 ♀ [1827–1832].

As this plate was published in the period 1827–1832 it falls as a synonym to *Polyommatus melanops,* Boisd. (1828). Boisduval says that it was discovered at Aix in Provence by the Count de Saporta, from whom also doubtless Geyer received the specimens that he named *saportae.*

SATYRIDAE.

9. **Erebia triarius,** Prun.

Papilio bonellii, Hb. Plate 181, figs. 892, 893 ♂, 894, 895 ♀ [1824–1826].

This name has always been treated as a synonym of *Erebia evias*, God. (1823), the correct specific name of which Warren (1929, *Ent. Rec.*, **41** : 147) has shown to be *triarius*, de Prunner (1798). The types of *triarius* came from Exilles in Piedmont. In view of the fact that Hübner dedicated his species to Bonelli, it is likely that it was from Bonelli that he received his specimens. Bonelli lived at Turin, and probably took his specimens somewhere in the Alps of Piedmont. It is therefore probably correct to treat *bonellii*, Hb., as a synonym of nominotypical *triarius.*

10. **Agapetes larissa,** Boisd.

and

11. **Agapetes larissa herta,** Geyer.

Papilio larissa, Boisduval. Geyer, Plate 182, figs. 896, 897 ♂, 898, 899 ♀ [1827–1830].
Papilio herta, Geyer, Plate 183, figs. 900, 901 ♂, 902, 903 ♀ [1827–1830].

These names apply respectively to two subspecies of the species usually known as *Melanargia larissa*, Hb. It is now possible to clear up as follows the great confusion that exists in regard both to the date and authorship of these names and to the type localities of the insects to which they apply.

(*a*) Subspecies *larissa*, Boisduval.

As the date of this plate (plate 182) of Geyer's is 1827–1830 (ranking for priority as 1830) the authorship of the name passes to Boisduval, who gives an adequate Latin diagnosis under this name on page 21 of his *Europ. Lepid. Ind. Meth.*, which, though dated 1829, was, in fact, published by November 1828 (*teste* Sherborn). Unfortunately, Boisduval gave as the type locality of his *Satyrus larissa* the wrong locality, "Dalmatia," where the subspecies *larissa* does not occur, being replaced by *herta*, Geyer. Fortunately, he gives an indication by which it is possible to establish the true locality of *larissa*, in that he does not give the name as his own but attributes it to Parreyss. Writing in 1833, Boisduval (*Ic. hist. Lépidopt. Europe*, **1** (11 & 12 : 136) says that the name *larissa* dates from the voyage of Parreyss in the Ionian Islands. In the following year, Treitschke (1834 in Ochsenheimer, *Schmett. Europa*, **10** (1) : 40) states definitely that *larissa* was discovered by Parreyss in Corfu, the locality given five years earlier by Freyer (1829, *Beitr. Gesch. europ. Schmett.*, **2** (13) : 85). The position is therefore that the author of *larissa* is Boisduval, its date of publication is 1828 and its type locality is Corfu. Subspecies *freyeri*, Fruhst. (1917, *Soc. Ent.*, **32** : 33) based on Freyer's figures falls as a synonym of nominotypical *larissa*.

(*b*) Subspecies *herta*, Geyer.

This plate of Geyer's is the first publication of the name *herta*. This name was a ms. name of Dahl's. Lefebvre (1832, *Ann. Soc. ent. France*, **1** : 86) said that he had seen in Dahl's collection a series of *herta* taken in Dalmatia at Fiume and Ragusa. In the following year, the type locality of *herta* was confirmed by Duponchel (1833 in Godart, *H.N. Lépidopt. France*, Suppl. **1** (Diurnes) : 172), who stated that Geyer's figures were taken from specimens caught by Dahl in the neighbourhood of Fiume and Ragusa. Subspecies *adriatica*, Seitz (1908, *Macrolep.*, **1**: 116) from Dalmatia is a synonym of *herta*.

12. Hipparchia neomiris marmorae, Hb.

Papilio marmorae, Hb. Plate 164, figs. 814, 815 ♂, 816, 817 ♀ [1824–1826].

This Sardinian subspecies of *Hipparchia neomiris*, God. (1823), was also named *Papilio iolaus* by Bonelli in 1826. As the date range of plate 164 is "January 1824–September 1826," Hübner's *marmorae* should take precedence over Bonelli's *iolaus*, as the latter should be assumed to have been published on December 31st, 1826, the actual month of its publication in that year being unknown. It falls as a primary homonym of *Papilio iolaus*, Hb. (plate 178), also published in the period 1824–September 1826. Bonelli's specimens were taken by the Cavaliere Alberto della Marmora. As Hübner dedicated his insect to della Marmora, there is no doubt that like Bonelli he received his specimens from that collector. Bonelli's locality for his *iolaus*, "Sardegna, Monte Genargentu, 800–1000 m.," may therefore be transferred to Hübner's *marmorae*.

13. Hipparchia semele ichnusa, nom. nov.

Papilio semele, Linn., Hb., *nec* Linn. Plate 168, figs. 832, 833 ♂, 834, 835 ♀ [1824–1826].

This subspecies of *Hipparchia semele*, Linn. (1758), was described in 1826 by Bonelli as *Papilio aristaeus*. The latter name is invalid as it is a primary homonym of *Papilio aristeus*, Stoll (1780 in Cramer, *Uitl. Kapellen*, **4** (27) : 60) and of *Papilio aristeus*, Stoll (1781, *ibid.*, **4** (31) : 139). I therefore propose the name *Hipparchia semele*, Linn. ssp. **ichnusa*, nom. nov.** pro *Papilio aristaeus*, Bonelli. Bonelli's *aristaeus* was described from specimens taken in Sardinia on Monte Genargentu. Krausse (1912, *Arch. Naturg.*, **78** A. 9 : 159) described an aberration of this subspecies, taken in the same locality as *Satyrus semele* var. *rautheri*; but his description is so slight and the form he describes is so unlike *aristaeus* that his name *rautheri* cannot be regarded as available for this subspecies.

14. Hipparchia fatua, Frr.

Papilio allionii, Hb. Plate 165, figs. 818, 819 ♂ [1824–1826].

It is probable that *allionii* is a mistake on the part of the engraver for *allionia*, the name given by Fabricius (1781) to the Portuguese subspecies of the closely allied species *Hipparchia statilinus*, Hufn. (1766). It should in any case be treated as a primary homonym of Fabricius' name and sunk as a synonym of *Hipparchia fatua*, Frr.

15. Pararge megera lyssa, Frr.

Papilio lyssa, Frr. Geyer, Plate 186, figs. 114, 115 ♂ (r. 914, 915), 116, 117 ♀ (r. 916, 917) [1827–1830].

This subspecies of *Pararge megera*, Linn., is always attributed to Hübner, but as this plate (plate 186) of Geyer's was published in the period 1827–1832 (thus ranking for priority from 1832), the authorship of the name should be credited to Freyer, by whom it was published independently in 1829 (*Beitr. Gesch. europ. Schmett.*, **2** (12) : 66). Freyer gives no locality. In 1833 Boisduval (*Ic. hist. Lépidopt. Europe*, **1** (17 & 18) : 222) redescribed *lyssa*, which he attributes to Parreyss and which he says was found in Dalmatia. This should therefore be accepted as the type locality.

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* Ichnusa was the name applied by the Greeks to the island of Sardinia. It is an allusion to the resemblance in shape of the island to the print of a foot.

16. **Pararge megera paramegaera,** Hb.

Papilio paramegaera, Hb. Plate 170, figs. 842 ♂, 843, 844 ♀ [1824–1826].

This is the Sardinian subspecies of *Pararge megera*, Linn., which in 1826 Bonelli named *Papilio tigelius*. For the same reasons as those explained above in connection with *P. marmorae*, *tigelius* falls as a synonym of *paramegaera*.

17. **Pararge maera hiera,** Fab.

Papilio adrasta, Illiger. Hb., Plate 169, figs. 836, 837 ♂, 838, 839 ♀ [1824–1826].

This name is universally credited to Hübner as having been first published by him on this plate. In fact, however, as Ochsenheimer (1816, *Schmett. Europa*, **4 :** 137) points out, the name was first used by Illiger in 1807 in his edition of Rossi's *Fauna Etrusca* (**2 :** 231). Commenting on Herbst's plate 207, figs. 5 and 6 and Esper's plate 68, figs. 1 and 2, Illiger says that Hoffmansegg gave [apparently in ms.] the name *Papilio adrasta* to this insect, which was found in "*Germania transrhenana.*" Herbst gives no locality for his insect (a female), which he calls *Papilio megaera* var. Esper's figures, which are also called *Papilio megaera* var., represent a male (fig. 2) and a female (fig. 1) of *Pararge maera*, which he says (1781, *Die Schmett.*, **1** (Bd. 2), *Forts. Tagschmett* : 100) were taken at Schwalbach.

The name *adrasta* cannot, however, be applied to the Rhineland subspecies of *Pararge maera* for two reasons. In the first place, it is invalid, as it is a primary homonym of *Papilio adrastus*, Stoll (1780, in Cramer, *Uitl. Kapellen*, **4** (27) : 62). In the second place, the oldest valid name for the subspecies of *Pararge maera* found in the area stretching from Germany to Northern and Central France is, as pointed out by Verity (1929, *Bull. Soc. ent. France*, **1929 :** 187), *hiera*, Fab. This name is based upon the figures given by Schaeffer in his *Icones* on plate 58, figs. 2 and 3, which clearly represent the subspecies of *Pararge maera* discussed above.

This, as Verity observes, means that the species so long erroneously called *Pararge hiera*, Fab., requires another name. I do not, however, agree with his suggestion that *ominata*, Krulik. (1903), should be adopted for this purpose, as there is available the name *petropolitana*, Fab., published in 1787 (*Papilio maera* var., in *Mant.*, **2 :** 36, No. 373), which was presumably based on specimens taken near St. Petersburg (Leningrad).

NYMPHALIDAE.

18. **Argynnis elisa cyrene,** Hb.

Papilio cyrene, Hb. Plate 166, figs. 822, 823 ♂, 824, 825 ♀ [1824–1826].

This Sardinian subspecies of *Argynnis elisa*, God. (1823), was described under the same name by Bonelli in 1826. For the reasons given above, under *P. marmorae*, Hübner's publication should take precedence of that of Bonelli and the name should be attributed in future to Hübner. As in the case of *P.*

marmorae, Hübner probably received his specimens direct from della Marmora. It is possible that he received them with the ms. name *cyrene*.

19. **Melitaea deione,** Geyer.

Papilio deione, Geyer. Plate 192, figs. 947, 948 ♂, 949, 950 ♀ [1827–1832].

The subspecies of *Melitaea deione* figured by Geyer only occurs in Southern France, and even without any text there could be no doubt as to its type locality. The latter is, however, definitely settled by Duponchel (1834 in Godart, *H.N. Lépid. France*, Suppl. **1** (Diurnes) : 276), who says that this species was discovered at Aix-en-Provence by the Count de Saporta, who, he adds, noted its special characters as far back as 1826.

20. **Aglais urticae ichnusa,** Hb.

Papilio ichnusa, Hb. Plate 170, fig. 840 [1824–1826].

This name for the Sardinian and Corsican subspecies of *Aglais urticae*, Linn., is in exactly the same case as *Papilio cyrene* discussed above, and for the same reason should be attributed in future to Hübner and not to Bonelli. The type locality given by the latter is " Sardegna, sommita del monte Genargentu."

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ON THE INDO-AUSTRALIAN AND ETHIOPIAN SPECIES OF THE BRACONID GENUS *SPATHIUS* (HYMENOPTERA)

By D. S. Wilkinson,
(Entomologist, Imperial Institute of Entomology.)

[Read 3rd June, 1931.]

With Plate XXXVIII and Twelve Text-figures.

The following attempt at a revision of this interesting and polymorphic genus is the outcome of work that was necessitated when the Institute received for identification a number of species the names of which were urgently required for inclusion in an economic paper (see 1931, *Bull. Ent. Res.*, **22** : 259).

The writer is well aware that, owing to the omission from the key of such a large number of the previously described species, this revision is far from satisfactory; but the impossibility of recognising species from descriptions such as Szépligeti almost invariably published is well known to Hymenopterists. Although, however, it was found impracticable to include in the key those species given at the end of this paper, which species, it is believed, constitute the remainder of those described from the region under revision, every possible endeavour was made, by a strict scrutiny of all the literature, to avoid describing as a new species under a new name a previously known form; and one or two series in the writer's possession that appear to agree with some of Szépligeti's descriptions have been deliberately excluded from the present work.

Some mention should be made here with regard to the coloration of species in this genus and to the areation of the propodeon and the figures that have been prepared to illustrate this systematically important part of their anatomy. Colour has been found to be on the whole very variable, in fact so variable as to be of but little importance, and the colour descriptions that follow have not, in consequence, been drawn up with any great deal of care. It would seem that the smaller the specimen the more weakly is it coloured, to such an extent that in some series the smaller specimens (more often, but not always, the males) are almost wholly testaceous, whereas the larger ones are completely and strongly darkened to black. Colour *pattern*, however, has been found to be of certain value, and this character has been used in the key, though sparingly.

The areation of the propodeon has provided some important characters, and these have been extensively used. This areation, however, is variable within certain limits, and due regard should be paid to this fact when examining the illustrations. These, prepared under the writer's supervision expressly for this paper by that very well-known artist Engel Terzi, endeavour to express the propodeal areation of the species (as represented by the series in our possession) rather than that of the individual. It would have been too laborious a task to prepare for each drawing a camera-lucida sketch of each specimen, so one specimen was chosen whose areation appeared to represent the happy mean: this specimen has almost invariably been made the type of the species.

Finally, it should also be remarked that the writer was lucky enough, with Prof. Poulton's invaluable assistance, to trace the types of *ruficeps*, Smith, and of *femoralis* and *apicalis* of Westwood. These three species, the unique repre-

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sentatives of which were standing in the Hope Dept., Oxford University Museum, with only very meagre clues as to their identity, have been redescribed and figured : and it is thought that the value of this paper has thereby been appreciably enhanced.

The very excellent photographs of the wings were made by Mr. M. E. Mosely, to whom the writer is much indebted.

KEY TO THE SPECIES.

1. Species with wings vestigial . . . . 2.
Species with wings complete . . . . 4.
2. Scutellum not roundly conical; propodeon not strongly convex, completely areated; ovipositor sheaths shorter than abdomen (S. Africa) 1. *cursor*, sp. n.
Scutellum distinctly roundly conical; propodeon strongly convex, without areation; ovipositor sheaths longer than abdomen . . . . 3.
3. Vertex coriaceous; petiole slender, on the whole narrower than the combined lengths of scutellum and metathorax (S. Africa) 2. *apotanus*, sp. n.
Vertex smooth; petiole stout, on the whole broader than the combined lengths of scutellum and metathorax (Europe; Madeira) 3. *pedestris*, Wesm.
4. Vertex coriaceous . . . . 5.
Vertex transversely carinate or transversely striate . . . . 6.
Vertex smooth . . . . 24.
5. First abscissa of medial vein of fore-wing very noticeably decurved in a broad sweep and thus at some point closely approaching 1st abscissa of anal vein (Pl. XXXVIII, fig. 1) (Ceylon; India; Philippines; Rodrigues I.) 4. *bisignatus*, Walk.
First abscissa of medial vein of fore-wing not thus noticeably decurved (Pl. XXXVIII, fig. 7) (S. Africa) . . . . 5. *dissors*, sp. n.
6. Females with 2nd tergite smooth . . . . 7.
Females with 2nd tergite sculptured . . . . 11.
7. Ovipositor sheaths shorter than combined lengths of head, thorax, and abdomen . . . . 8.
Ovipositor sheaths longer than combined lengths of head, thorax, and abdomen . . . . 10.
8. All tibiae colourless at base (India) . . . . 6. *cavillator*, sp. n.
Tibiae not colourless at base . . . . 9.
9. Head definitely transverse; areation of propodeon more or less obscured by rugae (Borneo) . . . . 7. *leptoceras*, Cam.
Head almost cubical; areation of propodeon not obscured by rugae (Borneo) . . . . 8. *leptothecus*, Cam.
10. Female with petiole equal to or longer than combined lengths of remaining tergites (Java) . . . . 9. *alipes*, sp. n.
Female with petiole shorter than combined length of remaining tergites (S. Africa) . . . . 10. *bruesi*, nom. n.
11. Second tergite of females with well-marked, longitudinal, more or less parallel striation or carination . . . . 12.
Second tergite of females minutely rugose or coriaceous, or if aciculate then with the aciculation irregularly oblique, and/or transverse, or concentric 13.
12. Ovipositor sheaths longer than abdomen; median basal longitudinal carina of propodeon very considerably shorter than distance from its point of bifurcation to in line with emission of costulae (Borneo) 11. *striaticeps*, Cam.
Ovipositor sheaths shorter than abdomen; median basal longitudinal carina of propodeon about equal to distance from its point of bifurcation to in line with emission of costulae (Java) . . . . 12. *piperis*, Wilkn.

13. Second tergite of females at most with fine aciculation, this commonly elongate, wavy, parallel or concentric . . . . 14.

Second tergite of females minutely rugose, coriaceous, or reticulate . . 17.

14. Median basal longitudinal carina of propodeon at least as long as distance from its point of bifurcation to in line with emission of costulae . . . 15.

Median basal longitudinal carina of propodeon considerably shorter, barely half distance from its point of bifurcation to in line with emission of costulae . . . . 16.

15. Majority of tergites (excluding petiole) almost completely covered with fine, close, transverse, concentric striation (Malaya) . 13. *femoralis*, Westw.

Majority of tergites smooth (India) . . . . . . 14. *vulnificus*, sp. n.

16. Ovipositor sheaths equal to or rather longer than abdomen; flagellum yellowish at apex; femora and tibiae not testaceous basally (Borneo) 7. *leptoceras*, Cam.

Ovipositor sheaths equal to or shorter than abdomen; flagellum unicolorous; all femora and tibiae testaceous basally (India) 6. *cavillator*, Wilkn.

17. Areola of propodeon wanting . . . . 18.

Areola of propodeon present . . . . 20.

18. First abscissa of medial vein of fore-wing noticeably decurved in a broad sweep and thus at some point closely approaching 1st abscissa of anal vein (Pl. XXXVIII, fig. 6) (S. Africa) . . . . 15. *rusticulus*, sp. n.

First abscissa of medial vein of fore-wing not thus decurved . . . . 19.

19. Recurrent interstitial; propodeon without major carination; petiole longer than remainder of abdomen (St. Vincent) . . . . *terminalis*, Ashm.

Recurrent very definitely into 2nd cubital; propodeon with at least median basal longitudinal carina; petiole shorter than remainder of abdomen (Madeira). . . . . 16. *moderabilis*, sp. n.

20. Ovipositor sheaths shorter than abdomen . . . . 21.

Ovipositor sheaths longer than abdomen . . . . 22.

21. Petiole slender and more or less elongated; median basal longitudinal carina of propodeon elongate, longer than distance from its point of bifurcation to in line with emission of costulae (Borneo) 17. *apicalis*, Westw.

Petiole stout; in female median basal longitudinal carina of propodeon very short, much shorter than distance from its point of bifurcation to in line with emission of costulae (India) . . . 18. *elaboratus*, Wilkn.

22. Second tergite of female with minute reticulation, which extends into basal half of 3rd tergite; apical half of 3rd tergite with some transverse striation (India) . . . . 19. *festinans*, Wilkn.

Second and 3rd tergites coriaceous . . . . 23.

23. Carination of lateral occiput longitudinal, strong; pronotum medianly with a very well-marked, thin but strong, transverse ridge; at least 8 mm. long (Aru) . . . . 20. *ruficeps*, Smith.

Carination of lateral occiput transverse, weak; pronotum apparently without median transverse ridge; 3 mm. long (Borneo) 21. *spilopterus*, Cam.

24. Second tergite smooth . . . . 25.

Second tergite sculptured . . . . 27.

25. First tergite with numerous rugulae (S. Africa) . . 22. *laeviceps*, Brues.

First tergite with smooth, longitudinal carinae, otherwise more or less smooth . . . . 26.

26. Distance between facial depressions hardly greater than their distance from eyes (Japan) . . . . *fasciatus*, Walk.

Distance between facial depressions at least twice their distance from eyes (Java) . . . . 9. *alipes*, sp. n.

27. Median basal longitudinal carina of propodeon extremely short, considerably shorter than (less than half) distance from its point of bifurcation to in line with emission of costulae (India) . 23. *generosus*, Wilkn.
Median basal longitudinal carina of propodeon as long as or longer than distance from its point of bifurcation to in line with emission of costulae 28.
28. Female with 3rd tergite entirely smooth, or at most with certain extremely fine, indefinite aciculation basally . . . . 29.
Female with 3rd tergite very decidedly and almost wholly sculptured . . 30.
29. Ovipositor sheaths longer than abdomen (Europe) . . . . *exarator*, L.
Ovipositor sheaths shorter than abdomen (India) . . . 14. *vulnificus*, sp. n.
30. Median basal longitudinal carina of propodeon more than twice as long as distance from its point of bifurcation to in line with emission of costulae (Seychelles) . . . . 24. *scotti*, sp. n.
Median basal longitudinal carina of propodeon equal to or only just longer than distance from its point of bifurcation to in line with emission of costulae . . . . 31.
31. Apex of 3rd tergite not emarginate; 2nd cubital cell elongate, the 2nd abscissa of radial twice as long as 2nd transverse cubital, and considerably longer than half length of 3rd abscissa (46 : 23 : 66) (Borneo) 25. *testaceitarsis*, Cam.
Apex of 3rd tergite emarginate, the apex laterally being carried forward markedly; 2nd cubital cell stout, the 2nd abscissa of radial not twice as long as 2nd transverse cubital, and about half length of 3rd abscissa (36 : 22 : 70) (Ceylon) . . . . 26. *striolatus*, Cam.

1. **Spathius cursor**, sp. n.

♀. Red testaceous, the thorax and abdomen, particularly the latter, commonly darkened to blackish; flagellum in about basal third red testaceous, then becoming brown and, apically, dark brown, the apical six joints however red testaceous to colourless; palpi, trochanters and trochantines, and usually base of all tibiae, colourless.

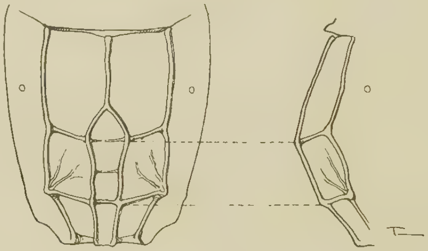

FIG. 1.—*Spathius cursor*, Wilkn., dorsal areation of propodeon: on right, lateral view.

♀. *Head* transverse with the eyes prominent; face weakly coriaceous and, occasionally, with some indefinite striation; facial depressions minute, their distance apart equal to their distance from the eyes; the grooves delimitating the clypeus very weak; the clypeus very short; eyes small, with length 1·2 times their breadth, this latter equal to the malar space; ocelli with distance from eyes quite five times distance between the posterior pair; frons, vertex, and median occiput, coriaceous and transversely striate, this combination sometimes giving a rugose effect; cheeks shining, indefinitely coriaceous; flagellum with 21–22 joints, the scape shorter than the 1st flagellar joint and equal to the 2nd. *Thorax :* mesonotum short, dull, coriaceous on the lateral lobes, coriaceous and more or less transversely rugose on the median anterior lobe, the crenulate notauli complete and converging posteriorly on a median area, which is definitely less strongly impressed than the notauli, and which has a single median longitudinal carina; the lower, horizontal, mesopleural sulcus, which is more or less complete, joining with the anterior, perpendicular, mesopleural sulcus, both sulci more or less definitely delimitated and not unduly broad, both crenulate and (apart from the crenulation) smooth and shining; the mesopleurae otherwise strongly coriaceous; the scutellum normal and only slightly convex; propodeon strongly coriaceous to granulate, with complete areation (fig. 1). *Wings* (Pl. XXXVIII, fig. 4) vestigial. *Abdomen:* 1st tergite inclined to be slender with the apex broadened and the spiracles prominent, shorter than the combined length of the remaining tergites; 2nd and succeeding tergites entirely smooth (save for a few setae); 2nd and 3rd tergites together longer than the combined length of the succeeding tergites; ovipositor sheaths shorter than the abdomen.

Length, 2·5–2·75 mm.

SOUTH AFRICA: Port St. John, Pondoland, 1 ♀, November 1923, 1 ♀, December 1923, 4 ♀♀ (one the *type*), January 1924, 1 ♀, 6–25.ii.1924, 1 ♀, 1–17.iii.1924 (*R. E. Turner*); Eshowe, Zululand, 1 ♀, 23–31.iii.1926 (*R. E. Turner*).

Type in the British Museum.

Host unknown.

2. **Spathius apotanus,** sp. n.

♀♂. Rather variable in colour according to size, the larger specimens more strongly (and thus more definitely) marked; red testaceous, very commonly with the thorax and abdomen strongly darkened to black; flagellum in about basal third red testaceous, then becoming brown and, apically, dark brown, the apical seven or eight joints however red testaceous to colourless; trochanters, majority of the middle coxae, basal half of the hind coxae, the base of all tibiae, more usually colourless.

♀♂. *Head* cubical with the eyes not prominent; face strongly coriaceous, with certain very widely spaced punctation; facial depressions often rather obscure, their distance apart equal to or rather less than their distance from the eyes; the grooves delimitating the clypeus definitely present; the clypeus long; eyes small, with length 1·26 times their breadth, this latter equal to the malar space; ocelli with distance from eyes in neighbourhood of 3·5 times distance between the posterior pair; frons and vertex almost smooth, or very weakly coriaceous, the median occiput more strongly coriaceous; in some larger specimens the coriaceous condition of the frons vertex and occiput is as strong as on the face, with in addition certain transverse striation on the frons; cheeks invariably shining and only very indefinitely coriaceous; flagellum with 21–27 joints according to size, more usually with 25; the scape just shorter than the 1st flagellar joint and equal to the 2nd. *Thorax:* mesonotum abnormally short, strongly coriaceous and dull, the notauli very short, very broad, not crenulate, and converging posteriorly on a median area, which is definitely less strongly impressed than the notauli, and which is without carination; the lower, horizontal, mesopleural sulcus, which is more or less complete though considerably narrowed posteriorly, and the anterior, perpendicular sulcus, both very broad, both internally not delimitated, both strongly coriaceous to granulate (as is the remainder of the mesopleurae), and crenulate to a varying degree of strength (often strongly crenulate and as often hardly at all), and combined to form a continuous, broad, depressed area occupying the anterior two-fifths and the lower fourth of the mesopleurae; the whole scutellum very distinctly roundly conical, and very distinctly more sharply declivous posteriorly than anteriorly or laterally; propodeon strongly coriaceous to granulate, usually with numerous strong rugae but without defined areation. *Wings* (Pl. XXXVIII, fig. 4) vestigial. *Abdomen:* 1st tergite slender with the apex somewhat broadened and the spiracles prominent, medianly to some extent swollen dorsally (but not laterally), shorter than the combined length of the remaining tergites; 2nd and succeeding tergites entirely smooth (save for a few setae), the larger specimens however exhibiting a certain indescribably minute roughness which makes the tergites rather dull; 2nd and 3rd tergites together in the ♀ equal to or longer than, in the ♂ considerably longer than, the combined lengths of the succeeding tergites; ovipositor sheaths longer than the abdomen.

Length : ♀, 2·0–4·0 mm.; ♂, 1·75–2·5 mm.

South Africa: Port St. John, Pondoland, 1 ♀, October 1923, 3 ♀♀, November 1923, 3 ♀♀, December 1923, 6 ♀♀, 5 ♂♂, January 1924, 2 ♀♀ (one the *type*), 3 ♂♂, 29.i.–5.ii.1924, 11 ♀♀, 6–25.ii.1924, and 2 ♀♀, 1–17.iv.1924 (*R. E. Turner*).

Type in the British Museum.

Host unknown.

The strength of the rugae on the propodeon varies considerably according to the size of the individual, the larger specimens having stronger rugae.

3. **Spathius pedestris**, Wesm.

Spathius pedestris, Wesmael, 1838, Nouv. Mém. Acad. Sci. Bruxelles, **11** : 132; Marshall, 1888, in André's Hym. Eur. Alg., **4** : 191.
Spathius apterus, Wollaston, 1858, Ann. Mag. Nat. Hist., (3) **1** : 24 (*syn. nov.*).

This species is known to me from a female previously in the Marshall collection and labelled *pedestris*, Wesm., and from three females from Madeira from the Wollaston collection, of which one is clearly the holotype of Wollaston's species.

Location of type unknown to me.

Host unknown.

4. **Spathius bisignatus**, Walk. (Pl. XXXVIII, fig. 1.)

Spathius bisignatus, Walker, 1860, Ann. Mag. Nat. Hist., (3) **5** : 309.
Spathius dinoderi, Gahan, 1925, Philipp. J. Sci., **27** : 84 (*syn. nov.*).

This species is known to me from Walker's type, a female, which was described from Ceylon; from a series of 4 ♀♀, 1 ♂, Rodrigues I., viii–xi.1918 (*H. J. Snell* and *H. P. Thomasset*); and from the following series from India :—Najibabad, United Provinces, 8 ♀♀, 5 ♂♂, 31.vii.1930, 5–25.viii.1930 (*R. N. Mathur*); Dehra Dun, 1 ♀, 1 ♂, 11.v.1922 (*C. F. C. Beeson*); Palghat, Madras, 1 ♀, 2.vi.1930 (*J. C. M. Gardner*); Jawalapur, Saharanpur, United Provinces, 1 ♀, 1 ♂, 19.v.1926, 24.vii.1926 (*N. C. Chatterjee*), 1 ♀, 1 ♂, 28.vi.1927, 14.vii.1927 (*B. M. Bhatia*). Of these series from India I forwarded to Dr. A. B. Gahan some specimens, at that time not having examined Walker's type; these were very kindly compared by Gahan with his type series of, and identified as, *dinoderi*, which species was originally described from two males from the Philippine Is.

Type in the British Museum.

Host. Walker's original description is without host record; Gahan records *dinoderi* to have been bred from *Dinoderus minutus*, F., infesting bamboo; the material before me from Najibabad is labelled " ex bamboo," that from Dehra Dun as " ex *Albizzia procera*," that from Palghat as " ex *Albizzia lebbek*," and that from Jawalapur as " ex *Dendrocalamus strictus*."

An undetermined species of *Spathius* is recorded by Ishii (1930, Oyo-

Dobuts.–Zasshi, **2** : 148–149) to be a parasite of *Chilo simplex*, Butl., in the Philippines : this, I consider, in view of the above records, might well be *S. bisignatus*.

5. **Spathius dissors,** sp. n.

♀♂. Dark red, approaching red-black, the following parts much paler to stramineous :—antennae (except apically, and the suturing of the flagellum), front coxae and trochanters (but not the trochantines), middle coxae, hind coxae in basal half, posterior trochanters and trochantines, all tibiae at base, anterior tibiae apically, basal half of basal joint of all tarsi, the basal two-fifths of the stigma, and basal half of ovipositor sheaths; ovipositor red; fore-wings (Pl. XXXVIII, fig. 7) with large areas deeply infumated; hind-wings lightly infumated; wing-veins and apical three-fifths of stigma dark red-brown.

♀♂. *Head :* face very definitely coriaceous, and with evenly and widely spaced punctation; facial depressions well marked, their distance apart just a little greater than their distance from the eyes; the grooves delimitating the clypeus oblique, the clypeus thus long; a slight median facial protuberance extends from immediately above the clypeus to the antennal insertions; the clypeus apparently not coriaceous; eyes small, their length about 1·5 times their breadth, this latter about 1·5 times the malar space; ocelli with distance from eyes between 2·0 and 2·5 times the distance between the posterior pair; frons and vertex normally as strongly coriaceous as the face (but without the punctation), often rather more weakly coriaceous; the occiput and cheeks, particularly the latter, weakly coriaceous, shining and thus contrasting with the face; flagellum with 28–38 joints, the scape equal to the 1st flagellar joint, longer than the 2nd. *Thorax :* mesonotum coriaceous and dully shining, without a median sunken area, the notauli definitely apparent only anteriorly (on the perpendicular sides and for a very short distance on the horizontal surface); the mesopleurae coriaceous and dully shining; the lower, horizontal, mesopleural sulcus present only in the anterior two-thirds, broad and shallow, not crenulate, and the anterior, perpendicular sulcus occurring as an area hardly apparent so broad and shallow is it and completely devoid of sculpture in any way differing from the remainder of the mesopleurae; propodeon with its dorsal areation weak and indefinite, save for a well-marked median longitudinal carina, which extends for about half the length of the propodeon, but even this extremely variable and often very short; in the apical third or fourth the propodeon has a mass of weak rugae, which occasionally indefinitely define an area; the somewhat obliquely raised costulae almost invariably present, as is the longitudinal carina laterally delimitating the large area on each side of the median carina, this latter about as strong as the lateral carina and as the costulae; propodeon otherwise, and apart from certain carination and rugosity laterally, coriaceous, with its apical margin strongly crenulate. *Wings :* fore-wing (Pl. XXXVIII, fig. 7) with the 1st abscissa of the medial vein not decurved nor closely approaching the 1st abscissa of the anal vein. *Abdomen :* 1st tergite stout with the spiracles more or less prominent, shorter than the combined length of the remaining tergites; 2nd and succeeding tergites exceedingly minutely and weakly rugose evenly throughout; 2nd and 3rd tergites together rather shorter than the combined length of the succeeding tergites; ovipositor sheaths equal to or rather shorter than the abdomen.

Length : ♀, 2·75–5·0 mm.; ♂, 2·75–4·25 mm.

South Africa : Port St. John, Pondoland, 2 ♀♀, 12–30.vi.1923, 1 ♀, 10–31.vii.1923, 1 ♂, 15–31.viii.1923, 1 ♀, September 1923, 6 ♀♀, 1 ♂, October 1923, 4 ♀♀ (one the *type*), 1 ♂, November 1923, 4 ♀♀, December 1923, 3 ♀♀, 2 ♂♂, January 1924, 1 ♀, 18–31.iii.1924 (*R. E. Turner*).

Type in the British Museum.

Host unknown.

6. **Spathius cavillator,** Wilkn. (Fig. 2.)

Spathius cavillator, Wilkinson, 1931, Bull. Ent. Res., **22** : 259.

This species is known to me from the original series, which consisted of 5 ♀♀, from Phanduwala, Dehra Dun, United Provinces, Kanchad, W. Thana, and Manon Range, N. Thana, Bombay, India.

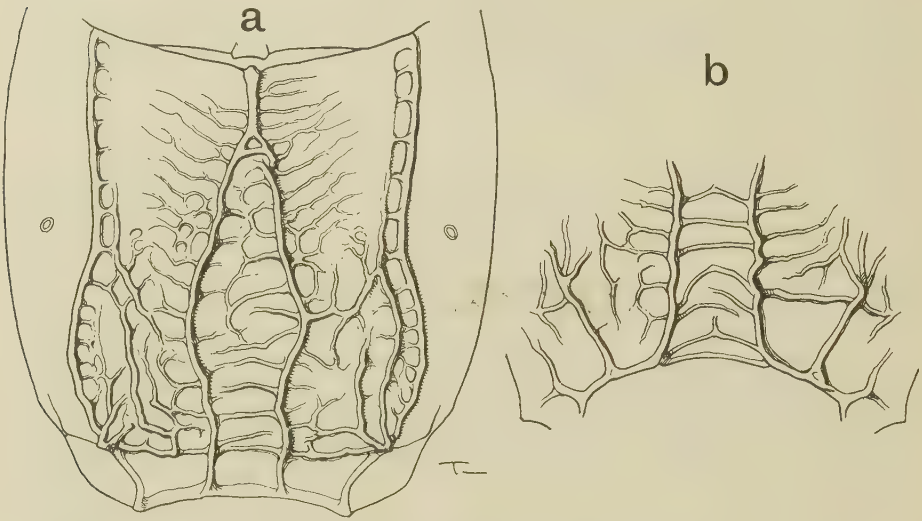

FIG. 2.—*Spathius cavillator*, Wilkn., dorsal areation of propodeon: *a*, dorsal view; *b*, postero-dorsal view.

Host. One specimen of the original series was labelled "ex *Thespesia populnea*," another "ex unknown climber," and the remainder, from which the type was selected, "ex *Terminalia belerica*."

7. **Spathius leptoceras,** Cam.

Spathius leptoceras, Cameron, 1908, Deuts. ent. Z., **1908** : 689.

This species is known to me from two females, both labelled in Cameron's writing as "type," which were described from Kuching, Borneo.

Type in the British Museum.

Host unknown.

8. **Spathius leptothecus,** Cam.

Spathius leptothecus, Cameron, 1908, Deuts. ent. Z., **1908** : 690.

This species is known to me from the type, a female, which was described from Kuching, Borneo.

Type in the British Museum.

Host unknown.

9. **Spathius alipes,** sp. n.

♀♂. Red testaceous; the thorax (except the neck, mesonotum, and scutellum), and petiole (except at extreme apex), black; majority of the abdomen (except at extreme apex), and usually also of the face, dark red-brown; ovipositor sheaths and tarsi red-brown, as is also the flagellum, which becomes increasingly more strongly darkened as the apex is approached; flagellum in ♀ occasionally with a pale band near apex; palpi colourless, as are often the anterior coxae with their trochanters and trochantines; wings evenly throughout and very definitely infumated, the hind-wings as strongly as the fore-wings; wing-veins and stigma red-brown, the latter with a very faint cloud basally.

♀♂. *Head:* face of ♀ with each lateral two-fifths transversely striate, the median fifth smooth, of ♂ almost invariably more or less entirely smooth save occasionally for some indefinite sculpture; facial depressions well marked, their distance apart three times their distance from the eyes; the grooves delimitating the clypeus run almost transversely, the clypeus thus very short; eyes with length about 1·2 to 1·3 times their breadth, this latter quite 2·5 times the malar space; ocelli with distance from eyes about 2·5 times distance between the posterior pair; frons of ♀ with fairly strong, transverse rugae, usually much more weakly sculptured in the ♂; vertex and median occiput invariably with at least some fine transverse striation, the striation often well marked and quite strong; cheeks shining and entirely smooth, as is the majority of the occiput; flagellum with about 35–40 joints (majority broken), the scape shorter than the 1st flagellar joint and rather longer than the 2nd. *Thorax:* mesonotum coriaceous and transversely rugose, with the notauli well marked and posteriorly converging on a large median slightly sunken area, which has two longitudinal, and a few transverse, widely spaced, carinae; the lower, horizontal, mesopleural sulcus complete, crenulate (except in some of the smaller specimens), and the anterior, perpendicular sulcus only weakly marked and with weak incomplete crenulation (absent in the smaller specimens); the mesopleurae otherwise smooth and shining; propodeon with the dorsal areation as figured (fig. 3), apart from this areation smooth and shining. *Wings:* fore-wing with the 1st abscissa of the medial vein not decurved nor closely approaching the 1st abscissa of the anal vein. *Abdomen:* 1st tergite slender, equal to or rather longer than the combined length of the remaining tergites; 2nd and succeeding tergites entirely smooth (save for a few setae); the 2nd and 3rd tergites together longer than the combined length of the succeeding tergites; ovipositor sheaths considerably longer than the combined lengths of the head, thorax and abdomen.

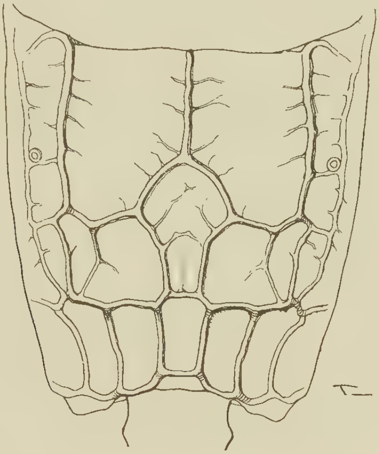

FIG. 3.—*Spathius alipes*, sp. n., dorsal areation of propodeon.

Length: ♀, 4 mm.; ♂, 2·5–3·0 mm.

JAVA: Tjibodas, 5,000–7,000 ft., 6 ♀♀, 13 ♂♂, August 1913 (*Dr. Koningsberger*).

Type in the British Museum.

Host unknown.

10. **Spathius bruesi,** nom. n.

Spathius striaticeps, Brues (*nec* Cameron), 1924, Ann. S. Afr. Mus., **19** : 11.

This species is known to me from a series in the British Museum from South Africa (Van Reenen, Drakensberg, Natal; Kloof, Natal; Umtata, Transkei; Port St. John, Pondoland; Gingindhlovu, S. Zululand) of 17 ♀♀, 5 ♂♂, determined as *striaticeps*, Brues, by, presumably, Turner, which apparently agrees sufficiently well with Brues' description.

This species was originally described from four females from Mfongosi, Zululand, and Acornhoek, Eastern Transvaal.

Host unknown.

11. **Spathius striaticeps,** Cam.

Meteorus striaticeps, Cameron, 1909, Soc. Ent., **24** : 108.

This species is known to me from the type, a female, which was described from Kuching, Borneo.

Type in the British Museum.

Host unknown.

The correct generic position of this species has not, I think, previously been published.

12. **Spathius piperis,** Wilkn. (Fig. 4.)

Spathius piperis, Wilkinson, 1931, Bull. Ent. Res., **22** : 264.

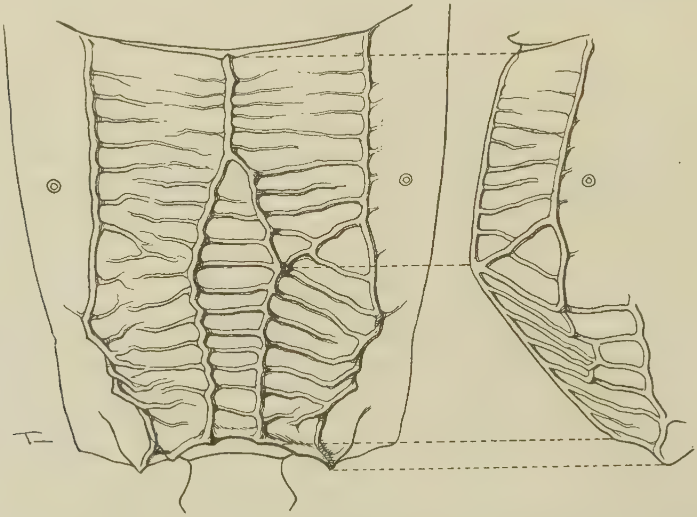

FIG. 4.—*Spathius piperis*, Wilkn., dorsal areation of propodeon: on right, lateral view.

This species is known to me from the original series, which consisted of 17 ♀♀, 10 ♂♂, from Pangkalpinang, Banka, Dutch East Indies.

Host. The original series was recorded as a larval parasite of the weevil *Lophobaris piperis*, Mshl., on *Piper nigrum.*

13. **Spathius femoralis,** Westw.

Stenophasmus femoralis, Westwood, 1882, Tijds. v. Ent., **25** : 43.

This species is known to me from the type specimen, a female, which was described from the island of Mysol in the Moluccas.

Type in the Hope Dept., Oxford.

Host unknown.

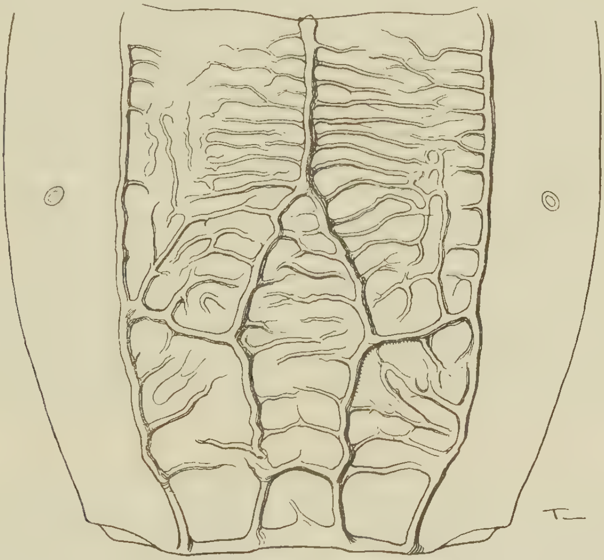

FIG. 5.—*Spathius femoralis,* Westw., dorsal areation of propodeon.

Through the kindness and assistance of Prof. Poulton I have been able to trace this type, and I now redescribe and figure it.

♀. Black; scape and about basal third of flagellum, all femora, all tarsi more or less, and the ovipositor, red or red testaceous; the anterior coxae, all trochanters, the basal third of the posterior tibiae, the palpi, the wing-insertions (but not the tegulae), and extreme apex of abdomen, stramineous; front tibiae, posterior tibiae otherwise than as above, all trochantines, basal joint of hind tarsus, the 5th joint of all tarsi, all veins in basal half of all wings (at least, the costal veins of the fore-wing), blackish to decidedly blackish; majority of remaining wing-veins, the flagellum apically, and the ovipositor sheaths, red-brown; stigma dark red-brown, pale in basal sixth, the extreme apex of the costal veins and the upper half of the upper portion of the basal vein equally pale; wings lightly infumated, with indications of a narrow hyaline band across the fore-wing beneath the base of the stigma; the fore-wing is strongly infumated between the stigma and the cubital vein, and also along both sides of both the lower portion of the basal vein, the apical third of the 1st abscissa of the medial, and the basal two-thirds of the 2nd abscissa of the medial vein.

♀. *Head:* face rugose, its median third together with the whole of the clypeus with transverse, more or less rugose carination; medianly in the upper third of the face is exhibited a narrow, perpendicular area that is entirely smooth; facial depressions well marked, their distance apart rather greater than their distance from the eyes (20 : 18); the grooves delimitating the clypeus well marked, oblique, the clypeus thus long; eyes with length 1·26 times their breadth, this latter twice the malar space; ocelli with distance from eyes just less than twice the distance between the posterior pair; frons with rather weak (but very definite), rather irregular, and fairly widely spaced carination; the whole of the vertex (even in the ocellar triangle) and the majority of the median occiput with strong, close, regular, transverse striation; some indefinite striation behind the eyes; cheeks shining and smooth, thus contrasting with the face; flagellum with at least 28 joints (*apex missing*), the scape considerably shorter than the 1st flagellar joint and definitely longer than the 2nd (23 : 28 : 20). *Thorax :* mesonotum coriaceous and shining, with the strongly crenulate notauli very strongly marked and posteriorly converging on a large median area (*pierced by pin*); both on the median anterior lobe down the middle, on the lateral lobes on each side, and down each side of the notauli, are short transverse carinae; the lower, horizontal, mesopleural sulcus weak but crenulate anteriorly, and posteriorly with certain indications of reaching the posterior margin; the anterior, perpendicular sulcus present as a very broad, sunken, strongly setiferous, rugose area occupying quite the anterior and upper two-fifths of the upper portion of the mesopleurae; mesopleurae otherwise shining and smooth with certain deep striae; propodeon with the dorsal areation and rugosity as figured (fig. 5), otherwise smooth and shining. *Wings :* fore-wing with the 1st abscissa of the medial vein not decurved nor closely approaching the 1st abscissa of the anal vein. *Abdomen :* 1st tergite fairly slender with the apex decidedly broadened and the spiracles prominent, shorter than the combined length of the remaining tergites; 2nd and succeeding tergites almost completely covered with fine, close but distinct, transverse, concentric and/or parallel striation; 2nd and 3rd tergites together shorter than the combined length of the succeeding tergites; ovipositor sheaths rather longer than the abdomen.

Length, 6·5 mm.

14. **Spathius vulnificus**, sp. n.

♀♂. Dark red testaceous to red-black; the head, scape, flagellum except apically, prothorax often, middle lobe of the mesonotum and the hind femora to some extent, legs otherwise, red testaceous; the male red testaceous almost throughout; palpi pale; wing-veins red-brown; the stigma dark brown to black in apical three-fourths, hyaline in basal fourth; fore-wings faintly infumated, more strongly so immediately beneath the apical three-fourths of the stigma and in the neighbourhood of the basal vein, hyaline in a narrow band across the wing beneath the basal fourth of the stigma.

♀♂. *Head :* face conspicuously swollen, striate throughout, the striae transverse and very fine and close together; facial depressions not well marked, their distance apart equal to their distance from the eyes; the grooves delimitating the clypeus only weakly oblique, the clypeus thus not long; eyes small, their length 1·35 times their breadth, this latter 1·33 times as great as the malar space; ocelli with distance from eyes about 2·5 (occasionally almost 3) times the distance between the posterior pair; frons, vertex (and in ocellar triangle), and median occiput, with fine, close, transverse striation, which is normally well marked but which is occasionally obsolete to entirely wanting, the vertex and median occiput in this latter case then smooth and shining; cheeks usually with some weak striation; flagellum with about 24–26 joints, the scape equal to the 1st flagellar joint and longer than the 2nd. *Thorax :* mesonotum coriaceous and shining, with the well-marked but weakly crenulate notauli converging on a large median sunken area, which has two or three fairly well-marked but rather irregular longitudinal carinae; the lower horizontal mesopleural sulcus present only in the anterior two-thirds, broad, rather shallow, normally with fairly strong crenulation, and the anterior perpendicular sulcus present as a broad area whose rugose carination rarely extends on to the upper half of the mesopleurae; mesopleurae otherwise shining, to some extent slightly coriaceous, commonly with much weak indefinite striation; propodeon with dorsal areation as figured (fig. 6), coriaceous where not carinate. *Wings:* fore-wing with the 1st abscissa of the medial vein not strongly decurved nor closely approaching the 1st abscissa of the anal vein. *Abdomen:* 1st tergite stout with the spiracles prominent, shorter than the combined length of the remaining tergites; 2nd tergite, and often certain basal portions of the 3rd tergite, with much fine aciculation, which is elongate, wavy, parallel and/or concentric; tergites otherwise smooth and shining; limitation of the apex of the 2nd tergite distinct, despite the 2nd suture being entirely wanting; 2nd and 3rd tergites together shorter than the combined length of the succeeding tergites; ovipositor sheaths shorter than the abdomen.

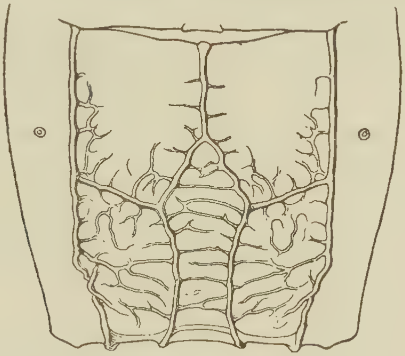

FIG. 6.—*Spathius vulnificus*, sp. n., dorsal areation of propodeon.

Length: ♀, 2·5–4·5 mm.; ♂, 2·5 mm.

INDIA: Rahatgaon, Hushangabad, Central Provinces, 2 ♀♀ (one the *type*), 1 ♂, 2–12.viii.1927 (*S. N. Chatterjee*), Jwalapur Saharanpur, 7 ♀♀, 29.iii.–31.v.1927, 14.vii.1927 (*B. M. Bhatia*).

Type deposited in the British Museum.

Host. The material from Rahatgaon is labelled " ex *Acacia catechu*," and that from Jwalapur " ex *Dendrocalamus strictus*."

15. **Spathius rusticulus**, sp. n.

♀♂. Dark red-brown to black, the following parts commonly rather lighter:—head, antennae (except for the suturing of the flagellum), all coxae in at least basal half, hind trochanters, all tarsi, and the basal two-thirds of the ovipositor sheaths; fore-wings (Pl. XXXVIII, fig. 6) with large areas deeply infumated; the stigma black in apical two-thirds, colourless basally; hind-wings almost entirely hyaline.

♀♂. *Head:* face conspicuously swollen, striate throughout, the striae tranverse and extremely fine and close together but stronger laterally; facial depressions more or less obsolete, their distance apart about equal to or rather less than their distance from the eyes; the grooves delimitating the clypeus run transversely, the clypeus thus represented solely by a carina between the grooves and the mouth; eyes small, their length 1·4 times their breadth, this latter equal to the malar space; ocelli close together, their distance from the eyes 2·5 times the distance between the posterior pair; frons, vertex, and occiput, striate throughout, the striation transverse, fine but distinct; flagellum with 22–26 joints, the scape rather shorter than the 1st flagellar joint and rather longer than the 2nd. *Thorax:* mesonotum coriaceous and more or less shining, the notauli definitely apparent only anteriorly (on the perpendicular sides) and only exceedingly weakly indicated on the horizontal surface where they converge posteriorly on a median area, which is very slightly sunken (if at all) and which only has some weak, rugose carination; the mesopleurae coriaceous and more or less shining; the lower, horizontal, mesopleural sulcus present only in the anterior two-thirds, weak and weakly crenulate, and the anterior, perpendicular sulcus present as an area hardly apparent so broad and shallow is it and so completely devoid of sculpture in any way differing from the remainder of the mesopleurae; propodeon with the dorsal carination represented only by the costulae, which are obliquely raised and invariably present, by the longitudinal carina laterally delimitating the large area on each side of the middle line, by the median longitudinal carina, which is present only at extreme base, and by a mass of fine rugae, which rarely even indicate an area; propodeon otherwise, and apart from certain carination and rugosity laterally, coriaceous and more or less shining, with its apical margin strongly crenulate. *Wings:* fore-wing (Pl. XXXVIII, fig. 6) with the 1st abscissa of the medial vein noticeably decurved in a broad sweep and thus at some point closely approaching the 1st abscissa of the anal vein. *Abdomen:* 1st tergite stout with the spiracles to some extent prominent, shorter than the combined length of the remaining tergites; 2nd and succeeding tergites evenly throughout very minutely and very weakly reticulate to exceedingly minutely and weakly rugose, weakly coriaceous on the sides; 2nd and 3rd tergite together about equal to or rather shorter than the combined length of the succeeding tergites; ovipositor sheaths with length about equal to that of the abdomen.

Length: ♀, 3·5–4·5 mm.; ♂, 3 mm.

SOUTH AFRICA: Port St. John, Pondoland, 1 ♀ (*type*), 15–31.v.1923, 1 ♂, September 1923, 1 ♀, November 1923, 1 ♀, January 1924, 1 ♀, 1–17.iii.1924 (*R. E. Turner*).

Type in the British Museum.

Host unknown.

16. **Spathius moderabilis**, sp. n.

♀♂. Largely stramineous to red-yellow testaceous, with the following parts commonly darkened to red-brown or nigrescent, or even black:—pronotum, suturing of the scutellum and metanotum, mesopleurae anteriorly and below, apex of propodeon, the petiole, large portions of the tergites, ovipositor sheaths, apical third of hind femora, about a median fourth of all tarsi, wing-veins, and apical half of stigma (the basal half being pale yellow); wings hyaline, broadly infumated along each side of the majority of the veins in the apical two-thirds of the fore-wing.

♀♂. *Head:* face transversely rugulose; facial depressions well marked, their distance apart somewhat less than their distance from the eyes; the grooves delimitating the clypeus oblique, the clypeus thus long; there is a slight median facial protuberance, which is smoother than the rest of the face; eyes small, their length 1·4 times their breadth, this latter equal to the malar space; ocelli very close together, their distance from the eyes 4·5–5·0 times the distance between the posterior pair; frons rugulose; vertex wholly, and occiput in the greater part, with coarse transverse striation giving a rugose effect; flagellum with 27–37 joints, the scape rather longer than the 1st flagellar joint, and this rather longer than the 2nd. *Thorax:* mesonotum coriaceous and dull, the weakly crenulate notauli well marked, rather broad and shallow, and posteriorly converging on a large median sunken area, which is irregularly rugose; the lower, horizontal, mesopleural sulcus present only in the anterior two-thirds, crenulate, and the anterior, perpendicular sulcus fairly broad and shallow and rugosely reticulate; the mesopleurae otherwise weakly rugose and particularly posteriorly with closely placed horizontal carination; propodeon with its dorsal areation weak and indefinite, save for a well-marked median longitudinal carina occupying the basal half; beyond this carina the propodeon has a mass of very weak rugae, which however do not define an area; the costulae rarely apparent; the longitudinal carina delimitating laterally the large area on each side of the median carina present only in about the basal third; propodeon otherwise, and apart from certain carination and rugosity laterally, coriaceous, and across its extreme apex with a series of foveae, or small impressed cells, whose margins are strongly bordered. *Wings:* fore-wing with the 1st abscissa of the medial vein not decurved nor closely approaching the 1st abscissa of the anal vein. *Abdomen:* 1st tergite stout, shorter than the combined length of the remaining tergites; 2nd tergite evenly throughout minutely rugoso-coriaceous, as is the 3rd tergite in the basal half or three-fifths but this latter very definitely more weakly so that the apical margin of the 2nd tergite is rendered distinct; 3rd tergite apically, and succeeding tergites, smooth or virtually so; 2nd and 3rd tergites together about equal to the combined length of the succeeding tergites; ovipositor sheaths considerably longer than the abdomen, as long as or nearly as long as the combined lengths of the head, thorax, and abdomen.

Length: ♀, 4·0–6·5 mm.; ♂, 2·5–3·5 mm.

MADEIRA: 6 ♀♀, 2 ♂♂, undated (*Wollaston*).

Type in the British Museum.

Host unknown.

This material was acquired by the British Museum by purchase in 1855.

17. **Spathius apicalis**, Westw.

Stenophasmus apicalis, Westwood, 1882, Tijds. v. Ent., **25**: 43.

This species is known to me from the type specimen, a female, which was described from Sarawak, Borneo.

Type in the Hope Dept., Oxford.

Host unknown.

Through the kindness and assistance of Prof. Poulton I have been able to trace this type, and I redescribe and figure it below:—

♀. Black; the legs dark red to red-black with all tarsi (except the 5th joint) red testaceous; anterior coxae and trochanters stramineous; face, scape, few basal joints of flagellum, and extreme apex of abdomen, red testaceous; flagellum otherwise red-brown (as are the ovipositor sheaths) becoming darker apically; ovipositor red; wings strongly infumated with the following areas in the fore-wing pale—wing insertions (but not tegulae)—an area sufficiently large to occupy the median fourth or fifth of the 1st abscissa of both the medial and anal veins—the upper third of the upper portion of the basal vein and the basal sixth of the stigma—a narrow transverse band across the wing beneath the base of the stigma—the apex of the wing embracing the apical third of the radial, apical half of the 3rd cubital, and apex of 2nd discoidal cells; wing-veins dark brown, with the remainder of the stigma and of the basal vein, together with the nervulus, the apical third of the 1st abscissa and the basal half of the 2nd abscissa of the medial vein, black.

♀. *Head:* face *obscured;* eyes with length 1·2 times their breadth, this latter twice the malar space; ocelli with distance from eyes just greater than twice the distance between the posterior pair; frons with rather weak (but very definite), rather irregular, and fairly widely spaced carination; the whole of the vertex (even in the ocellar triangle) and of the occiput with fairly strong, close, regular, transverse striation, save that in the neighbourhood of the eyes this striation becomes so fine as to be virtually finely rugose; the striation on the occiput extends laterally to behind the eyes where it bends forward strongly so that here it is not transverse but longitudinal; cheeks smooth and shining; flagellum with 43 joints, the scape shorter than the 1st flagellar joint and about equal to the 2nd. *Thorax:* mesonotum coriaceous and shining, with the crenulate notauli well marked and posteriorly converging on a large, median, slightly sunken area, which has two longitudinal, and some short and weaker, transverse, carinae; propodeon with the dorsal areation and rugosity as figured (fig. 7), otherwise indistinctly coriaceous and more or less shining. *Wings:* fore-wing with the 1st abscissa of the medial vein not decurved nor closely approaching the 1st abscissa of the anal vein. *Abdomen:* 1st tergite slender with the apex decidedly broadened, shorter than the combined length of the remaining tergites; 2nd tergite evenly and very definitely coriaceous and dull more or less throughout; 3rd tergite dull, coriaceous in about basal half, this sculpture so arranged that it is distinctly concentric, in about apical two-fifths with fine, very close, transverse (oblique laterally), concentric and/or parallel striation; 4th and 5th tergites much as in the 3rd, the succeeding tergites smooth; 2nd and 3rd tergites together shorter than the combined length of the succeeding tergites; ovipositor sheaths shorter than the abdomen.

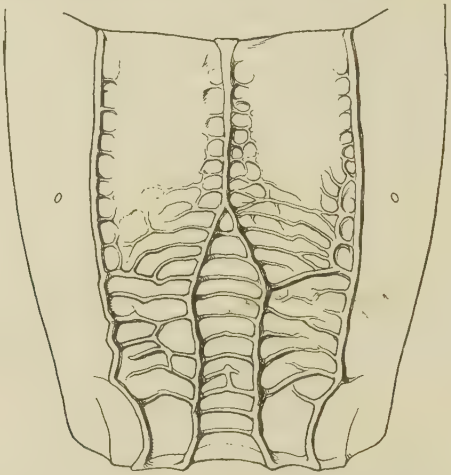

FIG. 7.—*Spathius apicalis,* Westw., dorsal areation of propodeon.

Length, 6·5 mm.

18. **Spathius elaboratus,** Wilkn. (Fig. 8.)

Spathius elaboratus, Wilkinson, 1931, Bull. Ent. Res., **22** : 260.

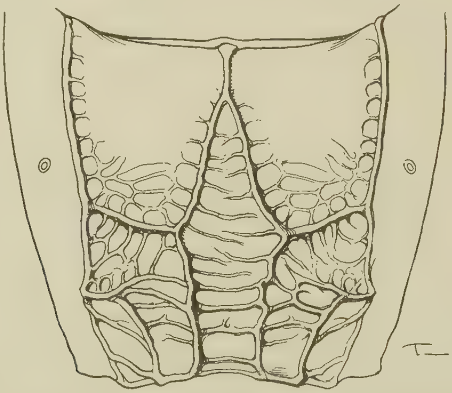

FIG. 8.—*Spathius elaboratus,* Wilkn., dorsal areation of propodeon.

This species is known to me from the original series, which consisted of 25 ♀♀, 7 ♂♂, from Jhajra and the Lachiwala Range, Dehra Dun, United Provinces, India.

Host. Some specimens of the original series were labelled "ex *Odina wodier*," others "ex *Vitis latifolia*," and the remainder, from which the type was selected, "ex *Ficus rumphii*."

19. **Spathius festinans,** Wilkn. (Fig. 9.)

Spathius festinans, Wilkinson, 1931, Bull. Ent. Res., **22** : 261.

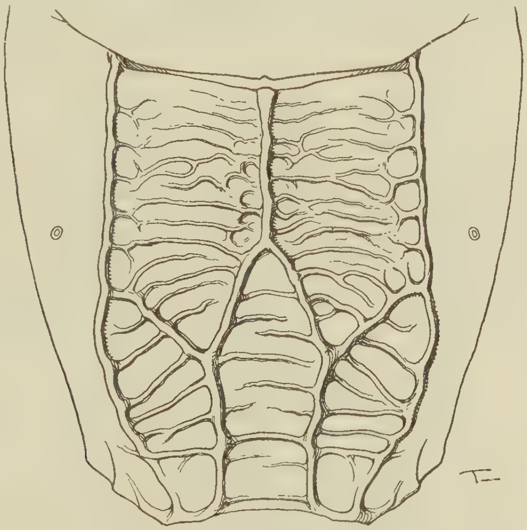

Fig. 9.—*Spathius festinans,* Wilkn., dorsal areation of propodeon.

This species is known to me from the original series, which consisted of 5 ♀♀, 1 ♂, from Koina R., Singhbhum, Bihar & Orissa, India.

Host. The original series was labelled "ex *Mangifera indica*."

20. **Spathius ruficeps,** Smith.

Stenophasmus ruficeps, Smith, 1858–59, Proc. Linn. Soc. (Zool.), **3** : 170; Westwood, 1882, Tijds. v. Ent., **25** : 42.

This species is known to me from the type specimen, a female, which was described from the island of Aru in the Moluccas.

Type in the Hope Dept., Oxford.

Host unknown.

Through the kindness and assistance of Prof. Poulton I have been able to trace this type, and I redescribe and refigure it below :—

♀. Black; head, scape, tarsi (except apical joint), and ovipositor sheaths largely (except towards apex), red testaceous; ovipositor red; front legs entirely, and majority of fore-wings, *missing ;* wing-veins dark brown.

♀. *Head :* face with transverse, more or less rugose carination; the clypeus not so strongly sculptured; facial depressions not well marked, their distance apart very definitely greater than their distance from the eyes; the grooves delimitating the clypeus not well marked, only weakly oblique, the clypeus thus not very long; eyes with length 1·27 times their breadth, this latter twice the malar space; ocelli with distance from eyes twice the distance between the posterior pair; frons with rather weak (but very definite), rather irregular, and fairly widely spaced, transverse carination; the whole of the vertex (even in the ocellar triangle) and of the occiput with strong, close, regular, transverse carination, which behind the eyes bends forward strongly so as to become not transverse but longitudinal; cheeks below this carination smooth and shining; flagellum *missing*. *Thorax:* mesonotum coriaceous and shining, with the crenulate notauli very strongly marked and posteriorly converging on a large median area (*pierced by pin*); both on the sides and posterior margin of the median anterior lobe, and on the sides of the lateral lobes to some extent, are short transverse carinae; the lower, horizontal, mesopleural sulcus definitely present in the anterior two-thirds where it is weak shallow and smooth but progressively broader and deeper posteriorly, and the presence of this sulcus in the posterior third of the mesopleurae indicated by a broad slightly sunken area with very strong transverse rugae; the anterior, perpendicular sulcus present as a very broad, sunken, very weakly sculptured and strongly setiferous area occupying quite the anterior and upper two-fifths of the upper portion of the mesopleurae; mesopleurae otherwise smooth and shining; propodeon with the dorsal areation and rugosity as figured (fig. 10), otherwise indistinctly coriaceous between the rugae, and shining. *Wings:* fore-wing with the 1st abscissa of the medial vein not strongly decurved nor closely approaching the 1st abscissa of the anal vein. *Abdomen:* 1st tergite slender, rather shorter than the combined length of the remaining tergites; 2nd tergite evenly and very definitely coriaceous and dull more or less throughout; 3rd tergite in basal half as 2nd, more weakly coriaceous and shining as the apex is approached; 4th and succeeding tergites coriaceous and shining; 2nd and 3rd tergites together shorter than the combined length of the succeeding tergites; ovipositor sheaths longer than the abdomen.

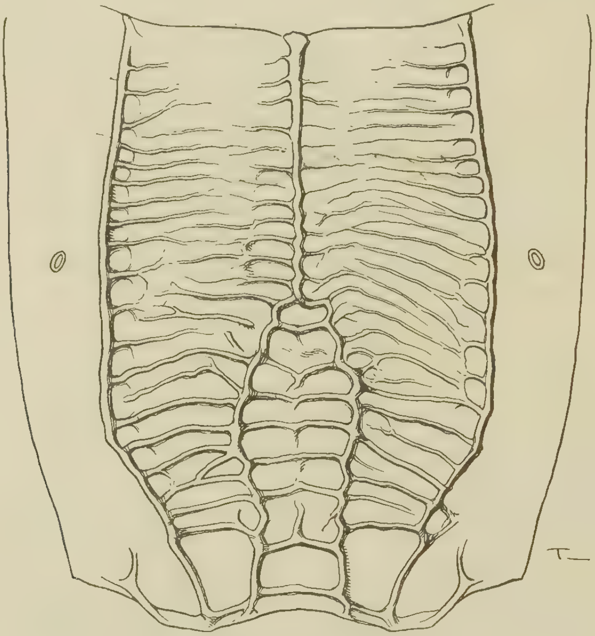

FIG. 10.—*Spathius ruficeps*, Smith, dorsal areation of propodeon.

Length, 10 mm.

Westwood's unnamed variety from Sula has the abdomen and legs virtually throughout more or less red testaceous, and the stigma pale in basal sixth, otherwise dark brown.

21. **Spathius spilopterus,** Cam.

Meteorus spilopterus, Cameron, 1909, Soc. Ent., **24** : 107.

This species is known to me from the type, a female, which was described from Kuching, Borneo.

Type in the British Museum.

Host unknown.

The correct generic position of this species has not, I think, previously been published.

22. **Spathius laeviceps,** Brues.

Spathius laeviceps, Brues, 1924, Ann. S. Afr. Mus., **19** : 13.

This species is known to me from a series in the British Museum from South Africa (Port St. John, Pondoland; Gingindhlovu and Eshowe, Zululand; Kloof, Natal) of 17 ♀♀, 1 ♂, determined as *laeviceps* by, presumably, Turner, which apparently agrees sufficiently well with Brues' description.

This species was originally described from apparently a single female from Komati Poort, Eastern Transvaal.

Host unknown.

23. **Spathius generosus,** Wilkn. (Fig. 11.)

Spathius generosus, Wilkinson, 1931, Bull. Ent. Res., **22** : 263.

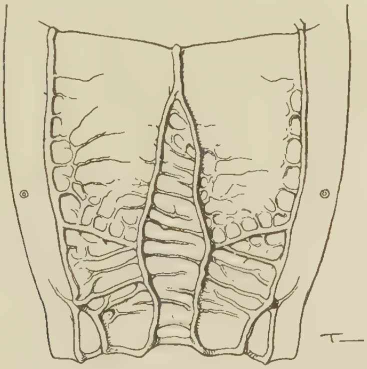

Fig. 11.—*Spathius generosus,* Wilkn., dorsal areation of propodeum.

This species is known to me from the original series, which consisted of 9 ♀♀, 1 ♂, from Deoban Range, Chakrata, India.

Host. The original series was labelled as having been bred out from a pole of *Cedrus deodara.*

24. **Spathius scotti,** sp. n.

♀♂. Black; scape, palpi, prothorax, tegulae more or less, wing-insertions, all coxae and trochanters and trochantines, the anterior femora, extreme base and apex of hind femora, extreme base of all tibiae, the ventrites (except the 1st), and the apical tergites (except in the male), red testaceous; tibiae otherwise, and tarsi, browned; the propodeon on the sides and to some extent apically, and sometimes the median lobe of the mesopleurae, red; the uniformly opaque stigma, the wing-veins, and the ovipositor sheaths, red-brown, the latter black apically; wings evenly throughout and very definitely infumated, the hind-wings as strongly as the fore-wings; hind femora of the smaller males red testaceous.

♀♂. *Head:* face with a median, slightly raised, fairly broad, longitudinal area, which below is nearly smooth and which above, though narrower, is entirely smooth, and alongside which the face is more or less reticulately rugose, the face being transversely rugose both in the lateral fifths, below, and on the clypeus; facial depressions not well marked, their distance apart rather greater than their distance from the eyes; the grooves delimitating the clypeus obscure but discernible, oblique, the clypeus thus long; eyes with length 1·5 times their breadth, this latter twice the malar space; ocelli with distance from eyes in ♀ twice the distance between the posterior pair, in ♂ rather less than twice; frons shining and entirely smooth, save occasionally for some exceedingly weak transverse striation, and, but very rarely, for a smooth narrow median longitudinal area reaching from the ocelli almost to the scrobes, this area not or hardly raised but delimitated by short transverse striation on each side; vertex, occiput, and cheeks shining and entirely smooth, thus contrasting with the face; flagellum with 42–46 joints in the ♀, 31–46 in the ♂, the scape longer than the 1st flagellar joint which is equal to the 2nd. *Thorax:* mesonotum coriaceous and shining, with the strongly crenulate notauli very well marked and posteriorly converging on a median, rather small, slightly sunken area, which has usually one median longitudinal carina but occasionally two, but these then almost invariably so close to each other as virtually to form one carina; the lower, horizontal, mesopleural sulcus complete, strongly crenulate, and the anterior, perpendicular sulcus usually not very well marked nor strongly crenulate (particularly on the smaller males); the mesopleurae otherwise smooth and shining; propodeon with the dorsal areation as figured (fig. 12), shining, in the area on each side of the median basal carina very distinctly coriaceous in the males but less distinctly so in the females. *Wings:* fore-wing with the 1st abscissa of the medial vein not decurved nor closely approaching the 1st abscissa of the anal vein. *Abdomen:* 1st tergite slender, rather shorter than the combined length of the remaining tergites; 2nd tergite in basal half finely rugose, the sculpture tending to form lines, in apical half with striation (or carination) that is transverse medianly and oblique to longitudinal laterally; 3rd tergite in basal three-fourths with

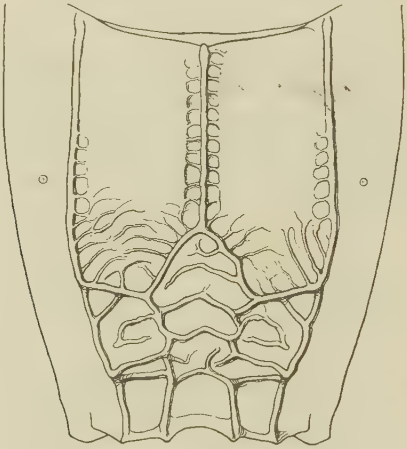

FIG. 12.—*Spathius scotti*, sp. n., dorsal areation of propodeon.

striation as on the apex of the 2nd tergite, here however as the apex is approached becoming increasingly fine, in apical fourth smooth and shining; succeeding tergites with occasional, very weak, transverse striation, mostly smooth and shining; 2nd and 3rd tergites together equal to or longer than, in the ♂ longer than, the combined length of the succeeding tergites; ovipositor sheaths considerably longer than, but not twice as long as, the abdomen, approaching, if not equal to, the combined lengths of the head, thorax, and abdomen.

Length : ♀, 5·0–6·25 mm.; ♂, 2·5–5·25 mm.

Seychelles Is. : Silhouette, Mare aux Cochons and forest above, circa 1,200 ft., 3 ♀♀ (one the *type*), 5 ♂♂, viii–ix.1908 (*Hugh Scott*) ; Mahé, near Morne Blanc, circa 1,000 ft., 3 ♂♂, xi.1908, Mare aux Cochons district, 1,000–2,000 ft., 1 ♂, i.1909, Cascade Estate, 1,000–2,000 ft., 2 ♀♀, 3 ♂♂, ii–iii.1909 (*Hugh Scott*).

Type in the British Museum.

Host unknown.

25. **Spathius testaceitarsis,** Cam.

Stenophasmus testaceitarsis, Cameron, 1908, Deuts. ent. Z., **1908** : 690.

This species is known to me from the type, a female, which was described from Sarawak, Borneo.

Type in the British Museum.

Host unknown.

26. **Spathius striolatus,** Cam.

Rhacospathius striolatus, Cameron, 1905, Spol. Zeylan., **3** : 86.

This species is known to me from the type, a female, which was described from Kandy, Ceylon.

Type in the British Museum.

Host unknown.

This species is a typical *Spathius*, and it is not understood why Cameron should have considered it necessary to erect a new genus for it. The genus *Rhacospathius* must be sunk, therefore; this synonymy has not, I think, previously been published, although recognised by Turner.

Species Unknown to the Writer.

27. **Spathius albiventris,** Szép.

Spathius albiventris, Szépligeti, 1905, Ann. Mus. Nat. Hung., **3** : 41.

Described from apparently a single female from New Guinea.

Location of type unknown to me.

Host unknown.

28. **Spathius albonervosus,** Motsch.

Spathius albonervosus, Motschulsky, 1863, Bull. Soc. Nat. Moscou, **36** (3) : 32.

Described from apparently a single male from Ceylon.

Location of type unknown to me.

Host unknown.

29. **Spathius antennalis,** Szép.

Spathius antennalis, Szépligeti, 1905, Ann. Mus. Nat. Hung., **3** : 40.

Described from apparently a single female from New Guinea.

Location of type unknown to me.

Host unknown.

30. **Spathius büttneri,** Stadl.

Stenophasmus büttneri, Stadelman, 1893, Ent. Nachricht., **19** : 226.

Described from apparently a single female from Togoland, West Africa.

Type in the " Museums für Naturkunde," Berlin.

Host unknown.

31. **Spathius caudatus,** Szép.

Spathius caudatus, Szépligeti, 1913, Ann. Mus. Nat. Hung., **11** : 599.

Described from apparently a single pair from Tanganyika Territory.

Type in the Hungarian National Museum.

Host unknown.

32. **Spathius flavicornis,** Szép.

Spathius flavicornis, Szépligeti, 1913, Ann. Mus. Nat. Hung., **11** : 599.

Described from apparently a single female from Tanganyika Territory.

Type in the Hungarian National Museum.

Host unknown.

33. **Spathius fulvus,** Szép.

Spathius fulvus, Szépligeti, 1905, Ann. Mus. Nat. Hung., **3** : 42.

Described from apparently a single female from New Guinea.

Location of type unknown to me.

Host unknown.

34. **Spathius fuscipennis,** Ashm.

Spathius fuscipennis, Ashmead, 1905 (1906), Proc. U.S. Nat. Mus., **29** : 119.

Described from a single male from Manila.

Type in the United States National Museum.

Host unknown.

35. **Spathius iridescens,** Schlett.

Stenophasmus iridescens, Schletterer, 1890, Berlin. ent. Z., **33** : 203.

Described from an unstated number of males from Australia.

Type. According to Schletterer the " typical specimens " are in the Natural History Museum, Vienna, and also in the Saussure collection ; this latter collection, Dr. Ferrière tells me, is in the Museum, Geneva.

Host unknown.

36. **Spathius javanicus,** Szép.

Spathius javanicus, Szépligeti, 1908, Notes Leiden Mus., **29** : 220.

Described from a single male from Java.

Type apparently in Szépligeti's collection.

Host unknown.

37. **Spathius manni,** Brues.

Spathius manni, Brues, 1918, Bull. Mus. Comp. Zool. Harvard, **62** : 102.

Described from apparently a single female from the Solomon Is.

Location of type unknown to me.

Host unknown.

38. **Spathius melleus,** Brues.

Spathius melleus, Brues, 1918, Bull. Mus. Comp. Zool. Harvard, **62** : 103.

Described from apparently a single female from the Solomon Is.
Location of type unknown to me.
Host unknown.

39. **Spathius minutissimus,** Szép.

Spathius minutissimus, Szépligeti, 1908, Notes Leiden Mus., **29** : 221.

Described from a single female from Java.
Type apparently in Szépligeti's collection.
Host unknown.

40. **Spathius minutus,** Szép.

Spathius minutus, Szépligeti, 1900, Termes. Füz., **23** : 55.

Described from apparently a single male from New Guinea.
Location of type uncertain.
Host unknown.

41. **Spathius pedunculatus,** Cam.

Spathius pedunculatus, Cameron, 1910, Wien. ent. Ztg., **29** : 93.

Described from a single female from Java.
Type in the Zoological Museum, Berlin.
Host unknown.

42. **Spathius pellitus,** End.

Spathius pellitus, Enderlein, 1912, Arch. Naturg., **78** A, (2) : 5.

Described from a single female from Sumatra.
Type in the Zoological Museum, Stettin.
Host unknown.

43. **Spathius philippinensis,** Ashm.

Spathius philippinensis, Ashmead, 1904 (1905), Proc. U.S. Nat. Mus., **28** : 148.

Described from apparently a single female from Manila.
Type in the United States National Museum.
Host unknown.

44. **Spathius pilosus,** Szép.

Spathius pilosus, Szépligeti, 1910, Notes Leiden Mus., **32** : 86.

Described from a single female from Batavia.
Type apparently in Szépligeti's collection.
Host unknown.

45. **Spathius pleuralis,** Szép.

Spathius pleuralis, Szépligeti, 1914, Mitt. Zool. Mus. Berlin, **7** : 193.

Described from apparently a single female from the Cameroons, West Africa.
Type presumably in the Zoological Museum, Berlin.
Host unknown.

46. **Spathius radialis,** Szép.

Spathius radialis, Szépligeti, 1908, Notes Leiden Mus., **29** : 221.

Described from a single female from Java.
Type apparently in Szépligeti's collection.
Host unknown.

47. **Spathius rufithorax,** Szép.

Spathius rufithorax, Szépligeti, 1914, Mitt. Zool. Mus. Berlin, **7** : 192.

Described from apparently a single female from Spanish Guinea.
Type presumably in the Zoological Museum, Berlin.
Host unknown.

48. **Spathius rufotestaceus,** Motsch.

Spathius rufotestaceus, Motschulsky, 1863, Bull. Soc. Nat. Moscou, **36** (3) : 31.

Described from apparently a single male from Ceylon.
Location of type unknown to me.
Host unknown.

49. **Spathius signipennis,** Walk.

Spathius signipennis, Walker, 1860, Ann. Mag. Nat. Hist., (3) **5** : 309.

Described from apparently a single female from Ceylon.
Location of type unknown to me; apparently it is not in the British Museum.
Host unknown.

50. **Spathius solox,** End.

Spathius solox, Enderlein, 1912, Arch. Naturg., 78 A, (2) : 5.

Described from a single female from Sumatra.
Type in the Zoological Museum, Stettin.
Host unknown.

51. **Spathius testaceus,** Szép.

Spathius testaceus, Szépligeti, 1913, Ann. Mus. Nat. Hung., **11** : 600.

Described from apparently a single female from Tanganyika Territory.
Type in the Hungarian National Museum.
Host unknown.

52. **Spathius transversalis,** Szép.

Spathius transversalis, Szépligeti, 1914, Mitt. Zool. Mus. Berlin, **7** : 193.

Described from apparently a single pair from Tanganyika Territory.
Type presumably in the Zoological Museum, Berlin.
Host unknown.

53. **Spathius trichiosomus,** Cam.

Spathius trichiosomus, Cameron, 1910. Tijds. v. Ent., **53** : 45.

Described from apparently a single female from Ceylon.
Type presumably in the Zoological Museum, Berlin.
Host unknown.

54. **Spathius tricolor,** Szép.

Spathius tricolor, Szépligeti, 1900, Termes. Füz., **23** : 55.

Described from apparently a single female from New Guinea.
Location of type uncertain.
Host unknown.

55. **Spathius tricoloratus,** nom. n.

Spathius tricolor, Szépligeti, 1914, Mitt. Zool. Mus. Berlin, **7** : 193 (*nec* Szépligeti, 1900).

Described from apparently a single female from Togoland, West Africa.
Type presumably in the Zoological Museum, Berlin.
Host unknown.

56. **Spathius trochanteratus,** Szép.

Spathius trochanteratus, Szépligeti, 1914, Mitt. Zool. Mus. Berlin, **7** : 193.

Described from apparently a single female from Spanish Guinea.
Type presumably in the Zoological Museum, Berlin.
Host unknown.

57. **Spathius variipes,** Szép.

Spathius variipes, Szépligeti, 1905, Ann. Mus. Nat. Hung., **3** : 41.

Described from apparently a single female from New Guinea.
Location of type unknown to me.
Host unknown.

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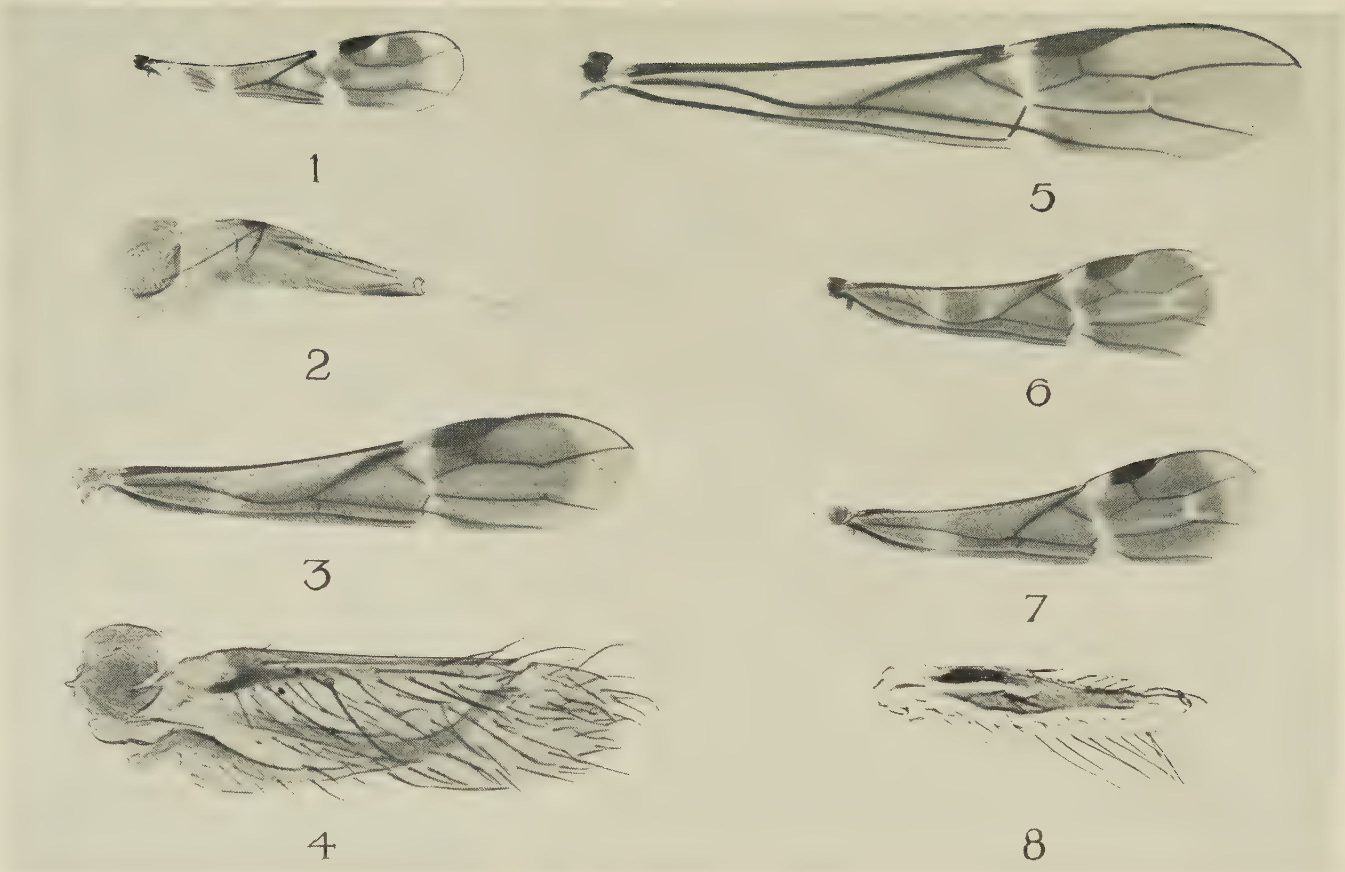

WINGS OF *SPATHIUS*.

Fig. 1. *S. bisignatus*, Walk.
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Fig. 4. *S. cursor*, sp. n.
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Fig. 6. *S. rusticulus*, sp. n.
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Fig. 8. *S. cursor*, sp. n., hindwing.

ADDITIONS AND CORRECTIONS TO THE AUTHOR'S "BUTTERFLIES OF JAMAICA (1926)"

By W. J. Kaye.

[Read 3rd June, 1931.]

With Plate XXXIX.

Since the publication of my "Butterflies of Jamaica" in 1926, *Trans. Ent. Soc. Lond.*, **1925** : 455-504, several people including myself have been exploring the Island to find additional species. As a result, there are here recorded another 15 species, raising the total to 106. Of these, two are entirely new, viz.—the Lycaenid, *Leptotes perkinsae* and the Hesperiid *Epargyreus perkinsi.* The former I have named after Miss L. Perkins and the latter after Mr. Perkins, both of whom have been instrumental in exploring the Lepidopterous fauna of the Island.

Thecla bourkei, now figured for the first time, was described by me in 1925, *Trans. Ent. Soc. Lond.*, **1924** : 416, but the locality given was Trinidad. It is now almost certain that the type did not come from Trinidad but from Jamaica, as Miss Perkins has since taken both sexes (singly only) on the northern slope of the hills near Jackson Town in Jamaica.

Nine out of the additional fifteen species are not found on the mainland except *Eupsyche martialis*, which reaches Florida. Four of the nine are not known outside Jamaica.

The species confined to Jamaica are : *Leptotes perkinsae, L. dominica, Thecla bourkei*, and *Epargyreus perkinsi.*

Four of the additional species have a wholly West Indian range—these are :—*Thecla celida, Calycopis angelia, Eupsyche martialis* and *Megalura eleucha.*

E. martialis just reaches Florida, while *T. celida* and *T. angelia* are also found in Porto Rico. *Megalura eleucha* only occurs in Cuba, Hispaniola and Jamaica. The statement in Seitz, Vol. V, p. 470, that it occurs in Texas and Florida is incorrect, the species present there being *M. peleus.*

The occurrence of a fourth species of *Danais—eresimus*—is remarkable. It has been taken on several occasions, but is usually rather rare. However, captures have been made as far apart as Bath and Claremont, indicating that it probably occurs over a large area.

In 1926, *Trans. Ent. Soc. Lond.*, **1925** : 458, I stated that "there is no mimicry between the families and genera." This may perhaps not be quite true, as an instance has occurred which looks very like mimicry or an approach of one species to another. Near Jackson Town *Lucinia cadma* and *Dynamine zetes* both occur rather commonly on the same ground. These two species when at rest with their wings closed have certain rather striking points of resemblance : hind-wing with a white ground-colour with two large eye-marks and double antemedian brown lines enclosing greyish scaling, a fore-wing with a large white sub-apical patch, and a whitish abdomen, etc., all of which are common to the two species. It is true the *Lucinia* is larger, but the difference in size is not very marked, as the *Dynamine* does not fold its wings so closely and shows a small portion of the costal area of the fore-wing, whereas the *Lucinia* depresses the fore-wing so as to be flush with the hind-wing. The *Dynamine* is certainly commoner than the *Lucinia*, and one would therefore surmise the approach to be by the *Lucinia*, though from the development of the large eye-marks this looks unlikely. Little help is to be derived from an inspection of the respective females, as these pretty closely approximate to the male colourings. The ♀ of *D. zetes* has the eye-marks slightly more separated than in the ♂, and this would suggest that *D. zetes* was the mimic. *Lucinia cadma* flies rather high up and settles on leaves and twigs of trees about 15–20 feet from the ground, while *Dynamine zetes* flutters near the ground and never settles more than 3–4 feet above it.

Danais eresimus.

Papilio eresimus, Cram., 1779, Pap. Ex., ii, t. 175, G.H.
Danais eresimus, Hnsch., 1909, *in* Seitz, Macrolep., V, p. 114.

Range of species : Venezuela, Colombia, Brazil, ? Central America.

Apparently rare, but most likely to a certain extent overlooked. The species is never common anywhere.

The larva has been found in Trinidad on *Spigelia anthelmia* (*W. Buthn*); Claremont (*L. Perkins*); Jamaica, probably Bath, in Aug. 1898 (*W. J. Kaye*).

[4. **Hymenitis diaphanus.**]

The larva of this species probably feeds on *Cestrum diurnum* (Solanaceae). In Cuba *H. cubana* (which is the representative of *H. diaphanus* in Jamaica) feeds on the above plant. It is a common shrub with white tubular flowers, which yield purple berries.

[5. **Heliconius charithonia charithonia.**]

On page 456 of my paper, "The Butterflies of Jamaica," 1926, *Trans. Ent. Soc. Lond.*, **1925**, a statement occurs in relation to this species that I have rectified in 1930 *Proc. Ent. Soc. Lond.*, **5** : 89. It is in relation to the mimic of *charithonia* in Hispaniola, where the female of *Dismorphia spio* in some of its varied forms sometimes becomes a very close mimic in exactly the same way as *Dismorphia cubana* ♀ does in Cuba. As so many of the Jamaican butterflies are rare and local, it is just possible there may be a *Dismorphia* as yet undiscovered.

Ageronia ferentina antillana.

Nymphalis ferentina, Godt., 1823, Enc. Méth., **9** : 428, n. 248.
Ageronia februa ferentina, Fruhs., 1916, *in* Seitz, Macrolep., V, p. 540.
Ageronia februa, Hübn., 1816–24, Samml. Exot. Schmett.
Ageronia februa antillana, Hall, 1925, Entomologist, **58** : 187.

Range of species : Mexico to S. Brazil, Hispaniola, Jamaica.

Range of subspecies : Hispaniola, Jamaica.

In Jamaica very rare. I have only one record of capture, viz. :—Baron Hill (*L. Perkins*).

The larva feeds on *Tragia volubilis*, "Vine nettle," and *Dalechampia pruriens*.

In Hispaniola Mr. Hall says the species is common up to 2000 ft.

The subspecies is founded on the spotting of the fore-wing being pure white and not grey and a similar difference in the hind-wing for the first two discal spots.

Megalura eleucha.

Markesia eleucha, Hübn., 1816–24, Samml. Ex. Schmett; 1818, Zutr. Ex. Schmett., pp. 197, 198.
Megalura eleuchea (*sic*) Seitz, 1921, Macrolep., V, p. 470.
Nymphalis pellenia, Godt., 1823, Enc. Méth., 9 : 359, n. 29.

Range of species : Cuba, Hispaniola, Jamaica.

Seitz in Macrolep., **5**: 470, gives south of the United States (Texas, Florida) as additional localities, but these are inhabited by the closely related *Megalura peleus* and not by *eleucha*, which is wholly West Indian.

A widely spread species but not common. It occurs at Mona, Bath, Jackson Town, Montego Bay. At Jackson Town it has been taken in June, July and August at about 500 ft. above sea-level. It also occurs at actual sea-level, but apparently does not reach any considerable altitude.

The female is considerably rarer than the male. It is much more ochreous brown and has no dark apical patch. There is also a straight postmedian transverse band to the fore-wing in addition to the bent median band.

The larva is apparently unknown. The closely related *M. peleus* is recorded as feeding on Cashew (*Anacardium occidentale*), and the author once found it on Mora in British Guiana.

[21. Lucinia cadma.]

In the neighbourhood of Jackson Town Miss Lilly Perkins has found this species occurring regularly in nearly every month of the year, although not commonly. On March 11th, 1930, I took two specimens in this same district. All efforts to find the larva have so far failed, but now that the imago has been taken somewhat frequently, there is certainly more chance of learning the life-history.

[35. Catopsilia statira.]

The race of *C. statira* in Jamaica is *hartonia*. It was described by Butler in *Trans. Ent. Soc. Lond.*, **1870** : 10. Mr. F. Martin Brown has kindly sent me his revision of the genus *Aphrissa*, into which section of *Catopsilia* he places the present insect. He separates *hartonia* as a distinct species, but neither his figures of the valva or uncus appear to justify separation from *statira* except subspecifically.

The synonymy is as follows :—

Catopsilia statira, Kaye, 1925, Trans. Ent. Soc. Lond., **1925** : 478.
Aphrissa hartonia, Martin Brown, 1931, Amer. Mus. Nov., **454** : 5.

I therefore call the Jamaican insect *Catopsilia statira hartonia.*

Chlorippe laure.

Papilio laure, Dru., Ill. Exot. Ent., 1773, ii, t. 18, f. 5, 6.
Chloripe laure, Röb. *in* Seitz, Macrolep., 1916, V, p. 547, Pl. 110 B.C.
Apatura laure, Dbl. Hew., Gen. Diurn. Lep., 1850, t. 42, f. 5.

Range of species : Mexico to South Brazil and Paraguay.

A very rare species in Jamaica. In Cuba there is a different species—*druryi*—and in Hispaniola there occurs a still more distinct species—*thoë.*

A female was recently seen at Jackson Town by Miss Perkins.

Jamaica often produces separate subspecies, while Cuba retains the mainland forms. *Papilio polydamas jamaicensis*, *Aganisthos odius orion* and *Coea* *acheronta cadmus* of Jamaica compare with *P. polydamas polydamas*, *A. odius odius* and *C. acheronta acheronta* from Cuba, these three latter forms also occurring in Central America. Again *Hymenitis cubana* from Cuba is much more like the mainland form *oto* than is *H. diaphanus* of Jamaica.

Terias nicippe.

Papilio nicippe, Cram., 1782, Pap. Exot., III, t. 210, c. d.
Colias nicippe, Godt., 1819, Enc. Méth., IX, p. 103, n. 43.
Xanthidia nicippe. Bois. Lec., 1833, Lep. Amer. Sept., p. 55, t. 20; Lec., 1836, Sp. Gén., 1, p. 653, n. 1.
Terias nicippe, Rob., 1910, *in* Seitz Macrolep., V, p. 81; Hall, 1925, Entomologist, **58** : 163.

Range of species. From New England to Northern Brazil, Cuba, Jamaica, Hispaniola.

Larva on *Cassia* spp.

In Jamaica very local and rather scarce. First discovered in Jamaica by Miss L. Perkins at Baron Hill, Jackson Town. Montego Bay, 12.3.30 (*W. J. Kaye*). It is essentially a lowland species and appears to be attached to the Northern side of the Island. In Hispaniola Mr. Hall gives a number of localities; it is also rather common in Cuba.

Family LYCAENIDAE.

Leptotes dominica. (Pl. XXXIX, figs. 1, 4, 7.)

Lycaena dominica, Moesch, 1886, Beitr. Schmett. Jam. p. 26, pl. 1, f. 10.
Hemiargus ammon dominica, Draudt, 1921, in Seitz, Macrolep., V, p. 820.

Range of species. Known only from Jamaica.

This little species, which is rare and perhaps to some extent overlooked, is quite distinct from *L. ammon*, which comes from Cuba and Florida. Draudt, in Seitz, makes *dominica* a subspecies of *ammon* and gives "Dominica" as the habitat. The specific name is rather misleading, for the island of Dominica does not produce the butterfly in question.

Moeschler does not quote any definite locality within the island of Jamaica. Apparently the species is very little known, for I have only seen but one or two specimens. Miss L. Perkins has recently secured a few in the neighbourhood of Jackson Town on the slopes facing the north coast. These have been taken in January, February and March, and on the 11th of that month in company with Miss Perkins I took one male in very fine condition. The female is evidently much rarer. *Leptotes cassius* is to be found flying in company with *L. dominica* and the two are inseparable on the wing.

L. ammon occurs in Hispaniola.

Leptotes perkinsae, sp. n. (Pl. XXXIX, figs. 2, 5.)

♂. Fore-wing above very similar to *L. cassius*, but a little more intensely coloured. Dark mauvy blue without any markings. Hind-wing above similarly coloured. No whitish marks in the lower discal area as sometimes seen in *L. cassius*. A rather large black spot showing through from the underside between veins 2, 3. Cilia white unspotted. Fore-wing below white with grey-brown markings. Two basal bands, the outer one not reaching costa followed by a short lineal spot. A median band reaching to vein 2 and a broader post-median band reaching to vein 3 followed by a short sub-apical mark. A marginal series of lunules containing linear spots. Hind-wing below white with a number of greyish-brown striae becoming less towards the marginal area. A series of marginal lunules containing curved spots. Towards the anal angle the last three lunules much larger and the middle one of these, *i.e.* between veins 2, 3, a large black spot surrounded with a narrow yellow ring. No inner second spot as in *L. cassius.* Exp. 22 mm.

Habitat: Jamaica, North coast, Baron Hill, June and September 1929 (*L. Perkins*), March 1930 (*W. J. Kaye*).

Callicista bubastus eurytulus. (Pl. XXXIX, fig. 13.)

This tailed form of *bubastus* is known to occur not uncommonly and is perhaps commoner than the non-tailed one. *C. eurytulus* is very similar to the female of *Calycopis angelia*, but is easily separable by the presence of a black spot ringed with whitish in the basal area of hind-wing. Further the median line is composed of black dots edged with whitish and not of black streaks edged with pure white. Dated specimens of *C. bubastus eurytulus* have been secured Nov. 1919, foothills; July 1919, at 600 ft., Kingston district (*D. F. W. Jackson*); Bath in August 1898 (*W. J. Kaye*); Mandeville in 1923 at 2000 ft.

Calycopis angelia. (Pl. XXXIX, fig. 12.)

Thecla angelia, Hew., Ill. Diurn. Lep., 1874, p. 162, n. 288, t. 63, f. 439, 440.
Thecla angelia, Draudt, 1920, *in* Seitz, V, p. 809, pl. 145 I.

Range of species. Cuba, Jamaica, ? Hispaniola.

Rather rare and apparently occurs chiefly on the northern side. At Jackson Town Miss L. Perkins has taken several specimens. This species is almost identical above with *Calycopis canus*, Druce, from Trinidad, Tobago and Venezuela, but beneath is quite different. Dated specimens of *T. angelia* have been taken in June 1928, August 1929 and February 1930, in all cases from Jackson Town.

Eupsyche martialis.

Thecla martialis, H.-S. 1864, Correspbl. Zool. Min. Ver. Regensb., **18** : 164.
Thecla martialis, Draudt, 1920, *in* Seitz, V, p. 780, pl. 155 G.

Range of species. Cuba, Jamaica, Hispaniola, Florida.

Not common. Taken near Jackson Town by Miss L. Perkins, and I have seen one or two other odd specimens. The species has a good deal of resemblance beneath to *Eupsyche acis*, which also occurs, but is also rather rare. *T. martialis* differs from *acis* below in having on the hind-wing the submarginal line consisting of a series of black dots above an orange patch, while in *acis* the submarginal line is broadly white edged with black beyond a red patch.

Thecla celida. (Pl. XXXIX, fig. 10.)

Thecla celida, Lucas, 1857, *in* Sagra Hist. Cuba, 7, p. 610.
Thecla celida, Draudt, 1920, *in* Seitz, V, p. 803, pl. 159 B.

Range of species. Cuba, Jamaica.

Only recently discovered in Jamaica by Miss L. Perkins, who has taken one or two on the north coast near Jackson Town. This is a very distinct little species with very faint wavy black markings on a pale blue underside of both fore- and hind-wing.

Thecla bourkei. (Pl. XXXIX, fig. 8.)

Thecla bourkei, Kaye, 1925, Trans. Ent. Soc. Lond., **1925** : 416.

Range of species. Perhaps confined to Jamaica.

The type locality was given as " Trinidad," but this has now been proved to have been an error. Miss L. Perkins has taken both sexes at Jackson Town, where the species is rare.

[47. **Papilio polydamas jamaicensis.**]

This species appears occasionally in considerable numbers. In March 1930 at Mandeville (2000 ft.), I found a wall where *Aristolochia trilobata* was growing, and around this there must have been about 25 *polydamas* flying. Most of them were females that were laying their eggs on the undersides of the leaves. At the foot of the wall, which enclosed a garden, there was a bed of garden " Nasturtiums," *Tropaeolum canariense*, and on these *polydamas* was also laying its eggs. I found several small batches, so the habit was a well-established one.

Family HESPERIIDAE.*

Subfamily HESPERIINAE.

Epargyreus perkinsi, sp. n. (Pl. XXXIX, figs. 16, 17.)

Fore-wing above russet brown, lightest in basal area, inclining to dark orange-golden. A squarish yellowish transparent spot lying within the end of cell, and immediately below it, between veins 2, 3, is another similar spot but much larger. Between veins 3, 4 is a triangular transparent spot midway between end of cell and outer margin, with a small linear transparent mark lying obliquely and touching the upperside of the triangular spot. A subapical transparent spot and three costal dots on the inner side. Hind-wing above of the same ground-colour as fore-wing with the costa broadly blackish-brown. Fore-wing below dark purplish-brown. In addition to the transparent spots there is a small orange basal spot. Hind-wing below dark purplish-brown. A well-marked post-median yellowish fascia faintly indicated towards costa but becoming well defined in lower half of wing. Two ill-defined short inner striae, yellowish mixed with brown. Between the innermost and the post-median striae the ground-colour is more purplish. Abdomen below dark blackish-brown. Exp. ♂ 60 mm., ♀ 66 mm.

Habitat: Jamaica, Baron Hill, 10.ix.29 (*L. Perkins*). There are also examples in the British Museum.

[77. **Rhinthon thermae.**] (Pl. XXXIX, fig. 14.)

This species described by me, 1926, *Trans. Ent. Soc. Lond.*, **1925** : 495, has not been figured before. The species is apparently very rare. There is a second specimen in the collection at the Institute of Jamaica.

[84. **Limochores insolata.**] (Pl. XXXIX, fig. 11.)

This rare species, which is peculiar to Jamaica, has been taken at Montego Bay at sea-level by Miss Greenly in the month of March. The female sex has

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* Whilst this paper was passing through the press E. L. Bell, 1931, *Ent. News, Philad.*, **42**: 220–222, has described another new species *Choranthus lilliae* from Bath.

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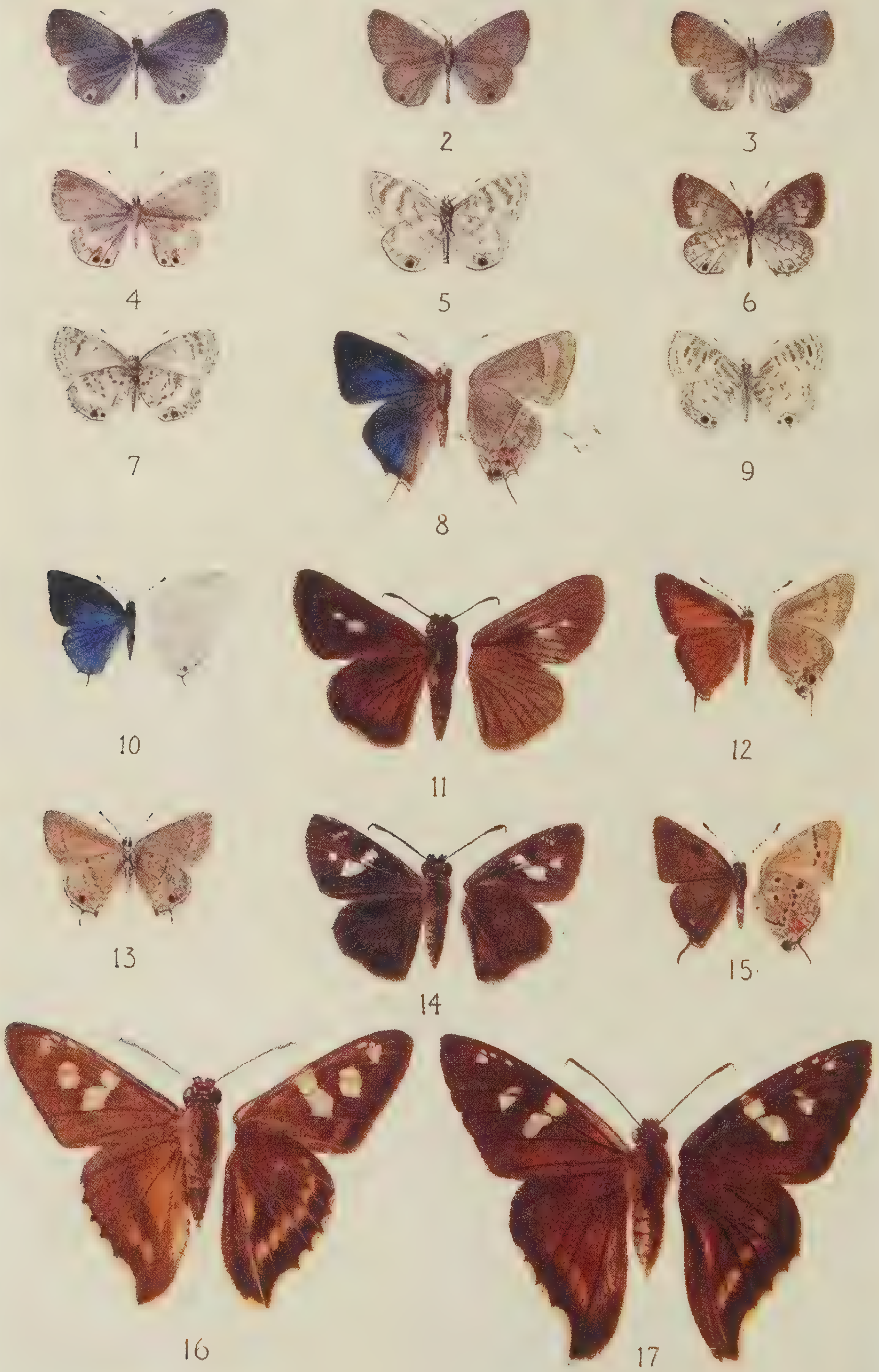
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Butterflies of Jamaica.

perhaps never been seen before, and I figure the specimen that Miss Greenly gave me soon after she had captured it.

Description of ♀ *Limochores insolata*, Butl.

Fore-wing above very dark brown with the base and basal inner margin ochreous. A large whitish hyaline squarish spot between veins 2, 3, and lying close to cell. A second very much smaller irregular spot between veins 3, 4, also close to cell. A minute white point between 6, 7. Hind-wing very dark brown with the inner two-thirds area with ochreous pubescence. No markings. Abdomen very dark brown with dark greenish pubescence. Fore-wing below light brown with the basal area black. The spots are less white below than above and the tornus is light coloured with a faint indication of an elongated white mark. Hind-wing below light brown without any marking. Abdomen below ochreous. Exp. 50 mm.

Epargyreus asander.

Eudamus asander, Hew., 1867, Desc. Hesp., p. 9, n. 13; Exot. Butts. *Eudamus*, t. 3, f. 24.
Epargyreus asander, Draudt, 1917, *in* Seitz, Macrolep., V, p. 861, Pl. 166, f.; Godm. and Salv., 1893, Biol. Cent. Amer. Rhop., ii, p. 300, Pl. lxxvii, f. 4.
Epargyreus antaeus, Kaye, 1925, Trans. Ent. Soc. Lond., **1925** : 492 (partim.).

Range of species. Mexico to Brazil.
Fairly common from sea-level up to 1000 ft.

EXPLANATION OF PLATE XXXIX.

FIG. 1. *Leptotes dominica*, Moesch. ♂.
4. ,, ,, ,, ♀.
7. ,, ,, ,, ♂ Underside.
2. *Leptotes perkinsae*, sp. n. ♂.
5. ,, ,, ,, ♂ Underside.
3. *Leptotes cassius* Cram. ♂.
6. ,, ,, ,, ♀.
9. ,, ,, ,, ♂ Underside.
8. *Thecla bourkei*, Kaye ♂.
10. *Thecla celida*, Lucas ♂.
11. *Limochores insolata*, Butl. ♀.
12. *Calycopis angelia*, Hew. ♂.
13. *Callicista bubastus eurytulus* ♂.
14. *Rhinthon thermae*, Kaye ♀.
15. *Callicista columella*, Fab. ♂.
16. *Epargyreus perkinsi*, sp. n. ♂.
17. ,, ,, ,, ♀.

ON SOME PECULIARITIES OF THE ABDOMINAL STRUCTURE IN CERTAIN MALE TRICHOPTERA

By H. Eltringham, M.A., D.Sc., F.R.S.

[Read 3rd June, 1931.]

With Plates XL and XLI and Three Text-figures.

Some years ago my friend Mr. Martin E. Mosely made the remarkable discovery of the male scent-organs in the genus *Hydroptila* and very kindly supplied me with material for the paper published in *Trans. Ent. Soc. Lond.*, **1919,** in which I described and figured the histology of these minute and complicated structures.

Further research on other genera and species of the smaller Trichoptera has been hampered by lack of fresh material. Large supplies of formol preserved material have been available, but hitherto our methods have not been successfully applicable to any material preserved in formol owing to the hardening action of this reagent when applied to chitin. Quite recently a preparation known as Diaphanol has been placed on the market, and I have found that, provided the chitin is not very dense, it can be sufficiently modified, by treatment with this fluid, to enable good sections to be obtained. As a result I am now able to describe certain very curious structures in species of other genera of the smaller Trichoptera. As in *Hydroptila* these features were originally discovered by Mr. Mosely, and I am once more indebted to him for the opportunity of investigating them.

The species so far examined belong to the genera *Diplectrona* (Hydropsychidae) and *Agapetus* (Rhyacophilidae). Cleared examples of *Diplectrona felix*, McL., mounted whole, showed that in the male abdomen there were four comparatively large bodies, apparently in the nature of vesicles, the walls of which are chitinous and beautifully reticulated. They lie ventro-laterally in the fifth and sixth abdominal segments. It seemed probable that they might be of a glandular nature, but the original examples in which they were observed had been treated with caustic, so that any glandular material, if originally present, would not have been preserved. Fresh material was secured and sections prepared. These, however, did not show any glandular structure whatever. Indeed the vesicles proved to be quite empty and provided with large canals or slits opening directly to the atmosphere. Such a condition indicated a tracheal origin, but at first no tracheal connection could with certainty be traced. Further series of sections, however, ultimately placed the tracheal interpretation beyond any doubt, and it is evident that for some purpose difficult to define, these insects have, in the male only, two large tracheal vesicles on each side. Plate XL, fig. 1, is a microphotograph of a section of part of the male abdomen of *Diplectrona felix.* The section, as also those shown in figs. 2 and 3, was made in a plane parallel to that of the expanded wings. The four tracheal vesicles, of which one is marked *TV*, in fig. 1, are distinctly seen with their reticulated supporting membrane and their direct openings to the exterior, one of which is marked *P* in fig. 2. *AG* is one of the large accessory glands of the genital apparatus which I shall describe later. In Plate XL, fig. 2, *T* is a trachea connecting directly with the adjacent vesicle. In fig. 3 the section has coincided with the surface membrane of one of the vesicles *TV*, and shows very clearly the reticulated structure, the function of which is doubtless to maintain the shape and expansion of the vesicle against the external blood pressure. These structures are not the same in number in all species, and there may either be four, as in *D. felix*, or two large vesicles with rudiments of the remaining pair, or in *Diplectronella*, originally separated as a species on account of the absence of fork 1 in the posterior wing, none at all.

Turning now to the genus *Agapetus* (RHYACOPHILIDAE), the material so far examined has included *A. fuscipes*, Curtis, *cyrnensis*, Mosely, and *nimbulus*, McL. These have two tracheal vesicles only, and they are of a somewhat different structure. The reticulation is absent and the necessary stiffening is provided by a thickening of the membrane. Plate XL, fig. 4, shows, at *TV*, the upper part of a vesicle not yet open to the exterior. *TS* is a testis, and between this and the corresponding testis of the other side can be seen a part of the intestine with the junction of the malpighian tubes. *AG*, *AG*, are portions of the accessory glands of the genital apparatus. In fig. 5 the form of the vesicle has begun to change, and a secondary vesicle, *SV*, appears. *TS* is again the testis. In fig. 6 the secondary vesicle has disappeared and the main structure *TV* has expanded and developed an internal septum. The shape and plications of these lateral vesicles in *Agapetus fuscipes* is so complicated that no mere verbal description would convey an adequate idea of their form. I have therefore made reflector drawings of a series of 48 consecutive sections taken in the plane of the expanded wings, and these are reproduced on Plate XLI. In fig. 1 a part of the trachea only is seen, but in 2 the section has touched the upper part of the vesicle where the trachea enters it. From 3 to 7 inclusive the dome-like structure expands and at 8 the opening to the exterior first appears. From 5 to 8 there is a small diverticulum at the anterior end. At 9 the large black area is the upper surface of a secondary vesicle which shows a gradual expansion up to section 14, where it develops an independent opening to the exterior. This opening persists as far as 18, but both it and the secondary vesicle itself disappear at 19. This secondary structure has no tracheal connection and seems to be merely a small diverticulum of the cuticle. It contains only air, and its function, if any, is quite obscure. From 16 to 22 the main vesicle develops internal projections which die out suddenly in 23. In 25 to 27 the anterior end develops small plications, and at 29 the section strikes the beginning of a deep fold, the two sides of which ultimately coalesce to form a septum, which persists as far as 44. The main opening to the exterior continues from 8 to 37, showing that it has the form of a long, more or less vertical slot. From 38 to 48 the vesicle is closed to the exterior and merely forms a downwardly projecting concavity.

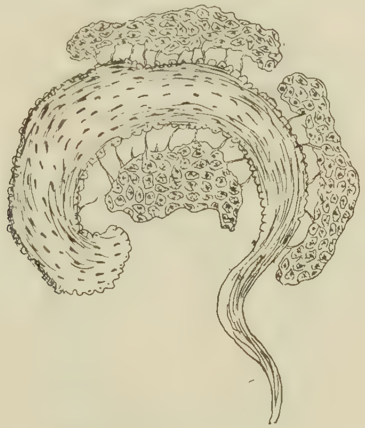
These peculiar structures are similar in the other species so far examined, but organs of a somewhat different type occur in species of which I hope soon to secure examples.

The meaning of these tracheal expansions, found as they are only in the male, is extremely difficult to imagine. So far as Mr. Mosely has been able to observe, the pairing habits, at any rate of *Agapetus fuscipes*, present no peculiar features. If the male pursued the female on or beneath the surface of the water, one might suggest some hydrostatic function, but skimming or diving do not appear to be involved. We know that in Mayflies the whole digestive tract is modified into an aerostatic apparatus, but the vesicles in

Diplectrona and *Agapetus* would not appear to afford a sufficient displacement volume to be of importance in this respect. There would seem to be a great opportunity for careful field observations, though the small size of the insects entails considerable difficulties.

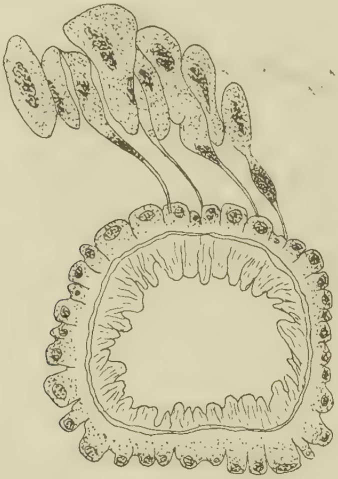
THE LATERAL GLANDS IN *AGAPETUS*.

The majority of my sections of *Agapetus* show the existence of an exceedingly small but very complicated structure lying in close proximity to the tracheal vesicles and just anterior to them. It appeared to me to be a glandular organ but of such unusual form that I invoked the aid of my friend Dr. A. D. Imms, F.R.S., to whom I am greatly indebted for valuable advice and suggestions. In the series of sections on Plate XLI, I have indicated more or less diagrammatically the position of this gland. The first trace of it appears in section 23, and at 25 its duct is connected with the external cuticle, though the actual opening to the exterior cannot in this series be observed. The opening is in fact so small that one is liable to miss it even in sections 4 μ thick. The gland disappears again at section 31. The apparatus consists of a convoluted duct, rather thick at its blind or proximal end but tapering distally towards its opening to the exterior. Lying massed round this duct is the gland tissue, consisting of heavily nucleated cells. These secretory cells are not in direct contact with the duct, but communicate therewith through a number of exceedingly fine ducteoles. Text-figure A is a purely diagrammatic representation of the organ, three masses of the glandular tissue being shown grouped round the curved and tapering duct. Text-figure B is a reflector drawing of a section from an example of *Agapetus cyrnensis* under the 1/2 in. immersion objective, passing transversely through the duct, and including a few cells of the gland with their ducteoles. The duct appears to be double in this section, having an outer layer of heavily nucleated cells and an inner stratum of fibrous material. This appearance is not common to all sections of the duct, and seems to occur most frequently near the distal end. It strongly suggests an invagination and a possible eversible property of the duct, though no example has yet been found with the part actually protruding.



A. Diagrammatic representation of the lateral gland and duct of *Agapetus*.

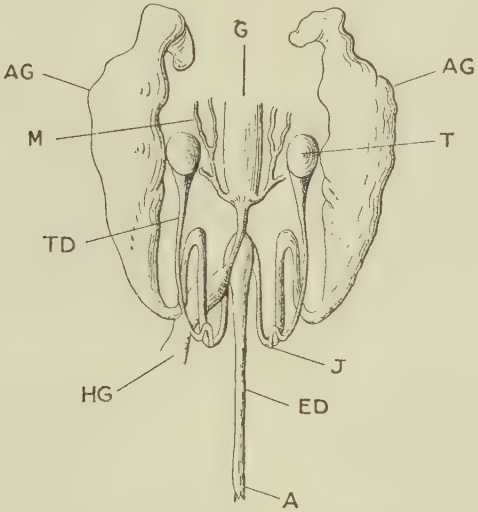
The cells of the gland tissue do not present any very complicated structure as found for instance in some Lepidopterous glands. The ducteoles are sometimes swollen and granular, suggesting the passage of a secretion. At their normal size they are about ·0003 mm. in diameter. Plate XL, fig. 7, shows a microphotograph of a section of part of the abdomen of *Agapetus cyrnensis* with portions of the gland and duct, though details cannot be seen at this magnification. Sections of the duct are marked *D*, *D*, and *G* is a small part of the gland. *O* points to three oenocytes which are nearly always present in association with the structure. Of the precise function of oenocytes we know very little, some authors having regarded them as excretory, and others as fulfilling functions analogous to those of the ductless glands in vertebrates. So far I have found this gland only in species of *Agapetus* and cannot discover any similar structure in *Diplectrona.* Occurring only in the males we must assume that it has some sexual function. Though it lies close to the tracheal vesicles already described, it does not communicate with them, and it is difficult to suppose any kind of co-operation between the two organs. Its form is quite unusual, the nearest structure bearing even a faint resemblance being, as Dr. Imms has suggested, the pygidial glands of some Coleoptera.



B. Reflector drawing of cross-section of duct of lateral gland in *Agapetus cyrnensis,* with a few cells of the gland and their ducteoles.

THE INTERNAL MALE REPRODUCTIVE ORGANS.

The internal organs of the smaller Trichoptera have apparently been but little studied. The dissection and sectioning of numerous examples has afforded an opportunity of examining them, and it seems desirable here briefly to record their arrangement. The most prominent feature is the comparatively enormous accessory glands. Text-figure C shows the general arrangement. The two testes, one of which is marked *T*, are quite separate, and their ducts, *TD*, open at *J* into those of the accessory glands *AG*, *AG*, shortly before these join the ejaculatory duct *ED*. The accessory glands occupy a large part of the body cavity. It is difficult to account for the presence of such large organs, unless pairing takes place several times by the same male. *A* is the aedeagus. Both the testis and accessory ducts are convoluted. In the figure, *G* is the intestine, *M* the malpighian tubes, of which there are, as usual in the Trichoptera, six branches, and *HG* is the hind-gut.



C. Internal organs of male *Agapetus fuscipes*. *G*, gut. *M*, malpighian tubes. *HG*, hind-gut. *AG*, *AG*, accessory glands. *T*, testis. *TD*, testis duct. *J*, junction of testis duct with that of accessory gland. *ED*, ejaculatory duct. *A*, aedeagus.

EXPLANATION OF PLATES XL–XLI.

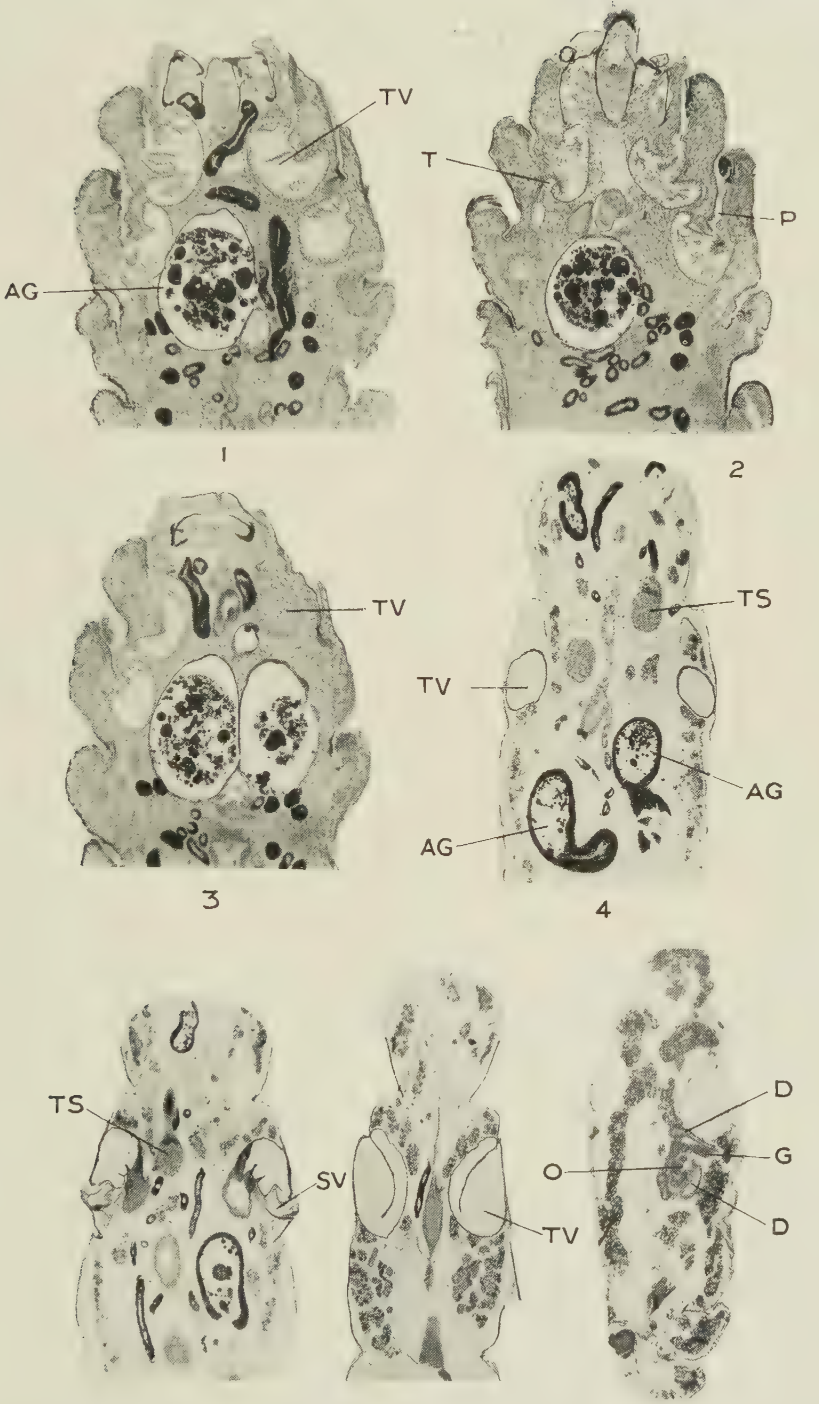
PLATE XL.

FIG. 1. Microphotograph of section of part of abdomen of male *Diplectrona felix*. *TV*, one of the four tracheal vesicles. *AG*, accessory gland of the reproductive system.

2. Ditto showing, at *T*, the tracheal connection with one of the vesicles. *P*, the passage to the exterior.
3. Ditto showing, at *TV*, the reticulated structure of the membrane of one of the vesicles.
4. Microphotograph of part of the abdomen of the male *Agapetus fuscipes*. *TS*, testis. *TV*, tracheal vesicles. *AG*, *AG*, accessory glands.
5. Ditto. *TS*, testis. *SV*, secondary vesicle.
6. Ditto. *TV*, tracheal vesicle.
7. Section of part of the male abdomen of *Agapetus cyrnensis*, showing part of lateral gland and duct. *D*, *D*, parts of duct. *G*, part of gland. *O*, oenocytes.

PLATE XLI.

A continuous series of 48 sections of the tracheal vesicle of a male *Agapetus fuscipes*. For description see text.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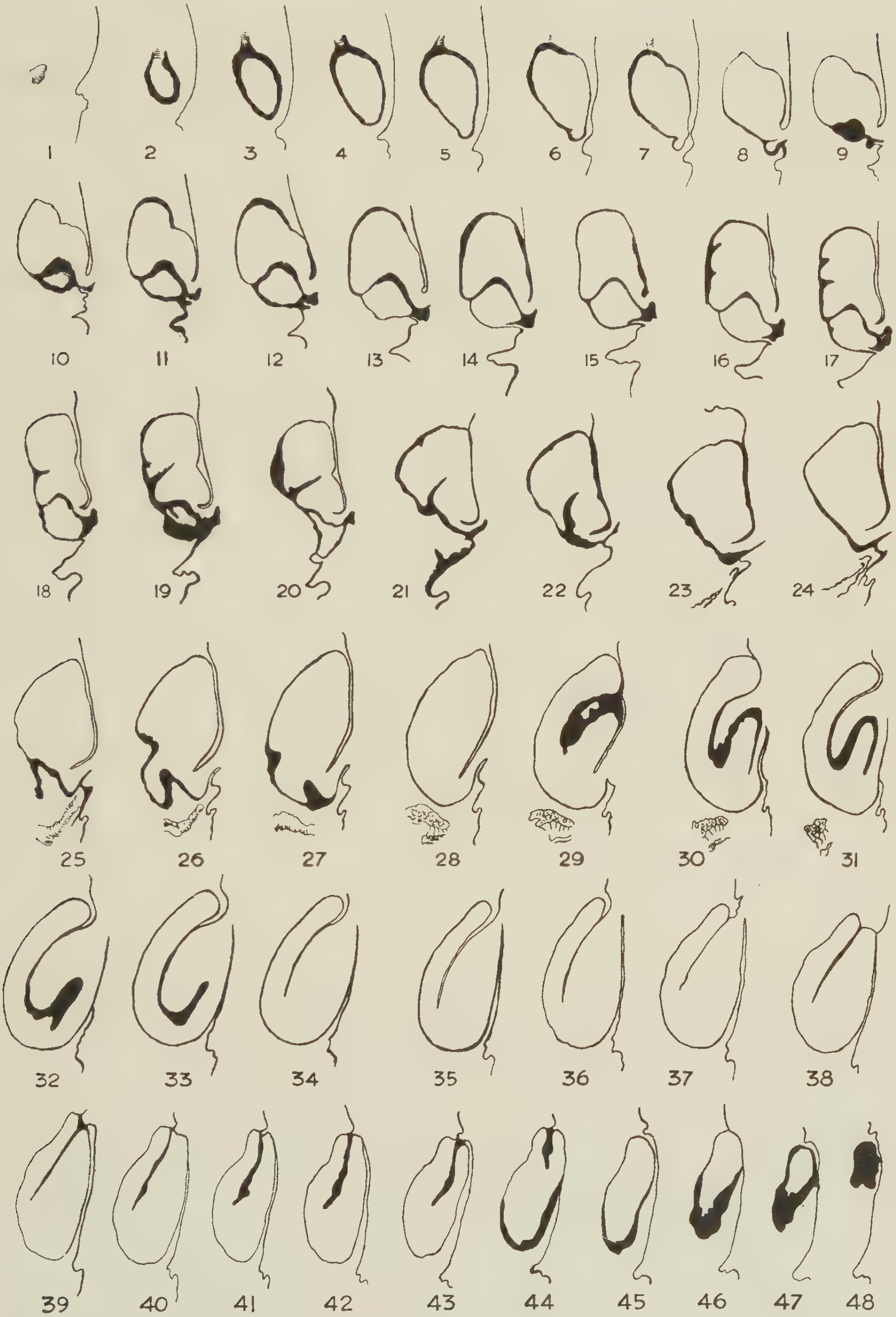
Tracheal Vesicles in Trichoptera.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Series of Continuous Sections of a Tracheal Vesicle of *Agapetus fuscipes.*

SOME NEW TRICHOPTERA FROM AFRICA AND BRITISH GUIANA

By M. E. Mosely.

[Read 3rd June, 1931.]

With Twenty-one Text-figures.

The species described as new in this paper were sent to the Imperial Institute of Entomology for determination and subsequently presented to the British Museum (Natural History) collection.

The new genus, *Psychomyiellodes*, is of special interest in that the inner spurs of the hind tibiae of the ♂ consist of two parts, a basal joint and a terminal claw, a formation hitherto described only in the genus *Dipseudopsis*.

Only one *Setodes* species has been recorded up to now in Africa, *Setodes gracilis*, but it is evident that there are many more species in this genus to be found on the Dark Continent, and there are several undetermined examples in the collection of the British Museum in addition to *Setodes squamosa*, sp. n., described here.

This paper is the first of a series dealing with the material sent to the Imperial Institute of Entomology, and I have to acknowledge the assistance received from Dr. Ulmer, of Hamburg, who has been kind enough to engage in a lengthy correspondence over the many points that have from time to time arisen.

The drawings for this paper have been made by Mr. D. E. Kimmins.

Atopsyche spinosa, sp. n. Figs. 1–5.

Head fulvous, clothed with fulvous hairs; antennae and palpi fulvous.

Wings: Anterior, yellowish brown with brownish pubescence; there are two patches of golden hairs, one where the sub-costa and the other where R meets the costa; cross-veins of the anastomosis white; a white diagonal streak below the basal angle of the discoidal cell and another just above the centre of the post-costa at A_2. Posterior wings uniformly brownish.

Legs yellowish brown.

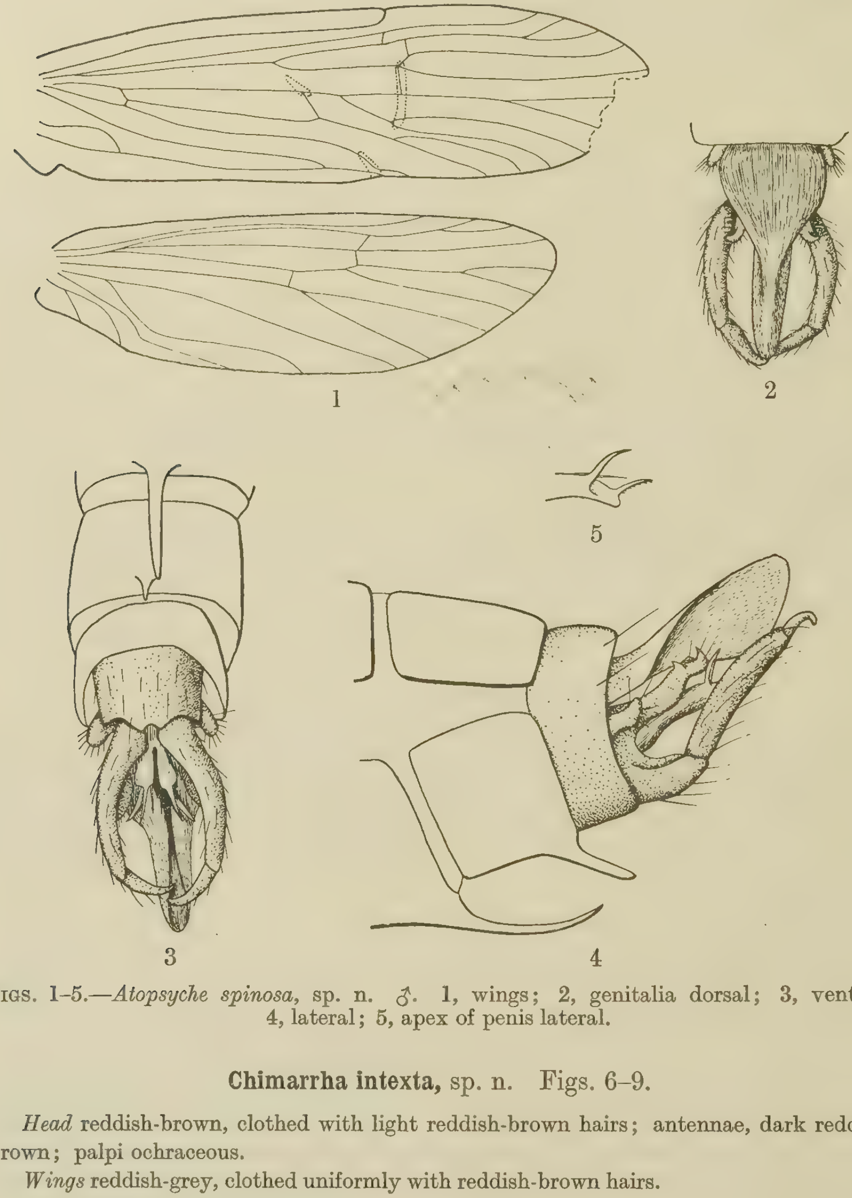
Abdomen brown above, yellowish-brown beneath.

Male genitalia: last dorsal segment produced in a long process, stout at the base, narrowing to a finger-like extension with a sub-acute apex, cleft beneath, the lateral margins towards the base extending outwards to make two shelves; from the side, the dorsal process is narrow at the base, dilating towards the apex. There are two short side-pieces terminating in rounded apices; upper penis-cover in the form of two short processes, the apices of which, from above, can be seen on each side of the dorsal process as short outwardly turned hooks fringed with stout bristles; from the side their upper margins, towards the apices, are furnished each with two strong upturned spurs, lower margins sinuous, dilated towards the base. Apex of penis from beneath, cleft and armed with pairs of long spines. Inferior appendages, two-jointed, basal joint long, terminal joint short, slender, with apex directed downward to make a slight hook. Margin of last sternite with a slight excision at centre; long curving process to the sixth ventral segment, and a short, straight process to the seventh.

Length of body, ♂, 4 mm; anterior wing, ♂, 6 mm.

BRITISH GUIANA; Kaieteur, 26.v.1929 (*A. Mackie*, per *T. D. A. Cockerell*).

Type ♂ (a balsam preparation), paratype ♂ and one example, sex unknown, with abdomen missing, in the British Museum collection.



FIGS. 1–5.—*Atopsyche spinosa*, sp. n. ♂. 1, wings; 2, genitalia dorsal; 3, ventral; 4, lateral; 5, apex of penis lateral.

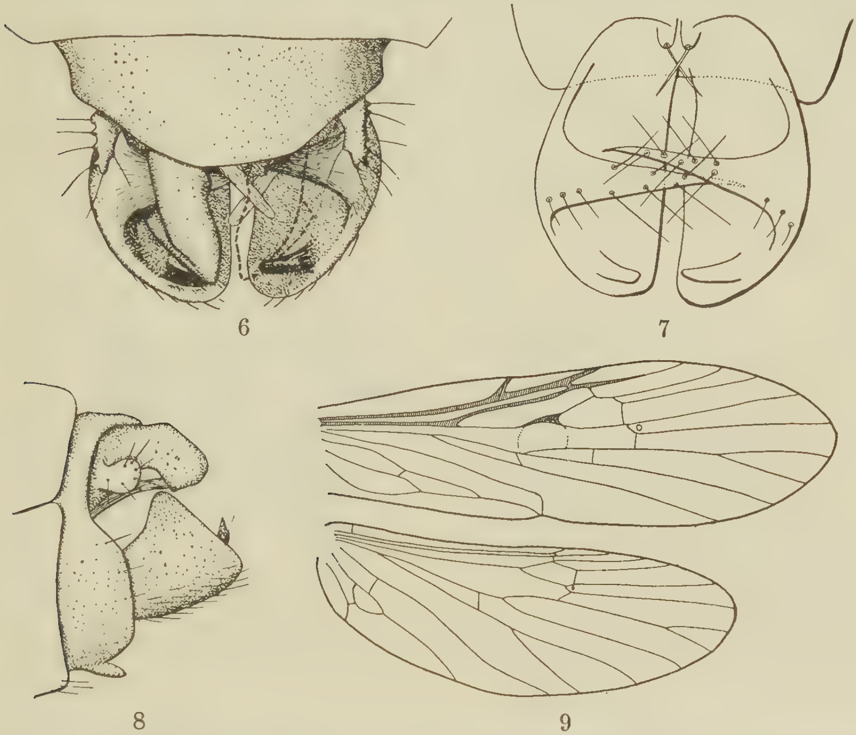
Chimarrha intexta, sp. n. Figs. 6–9.

Head reddish-brown, clothed with light reddish-brown hairs; antennae, dark reddish-brown; palpi ochraceous.

Wings reddish-grey, clothed uniformly with reddish-brown hairs.

Legs ochraceous.

Male genitalia : margin of terminal dorsal segment rounded. Superior appendages, one of which has been broken off in the type, from above, long, somewhat rectangular but narrowing to acute apices, seen from the side, curving downward, broad at the base, lower margins very concave, apices truncate; on each side of the appendages are short processes the margins of which, from above, are very serrate and from the side appear as rounded processes seated on broad bases. Inferior appendages very broad, concave; arising from their upper margins at the centre are two very long acute processes extending horizontally inwards and crossing each other; towards the apex of each appendage and from its inner surface arises a blackened process which is shorter than the marginal process and is also directed inward. At the base of the appendages, internally, are two small tubercles, each armed with a stout bristle. From the side, the inferior appendages are narrower at the base than at the apex, which is broadly truncate. Penis very broad with apex slightly dilated; from above, two semi-transparent penis sheaths can be seen, crossing each other. There is a short process to the terminal ventral segment.



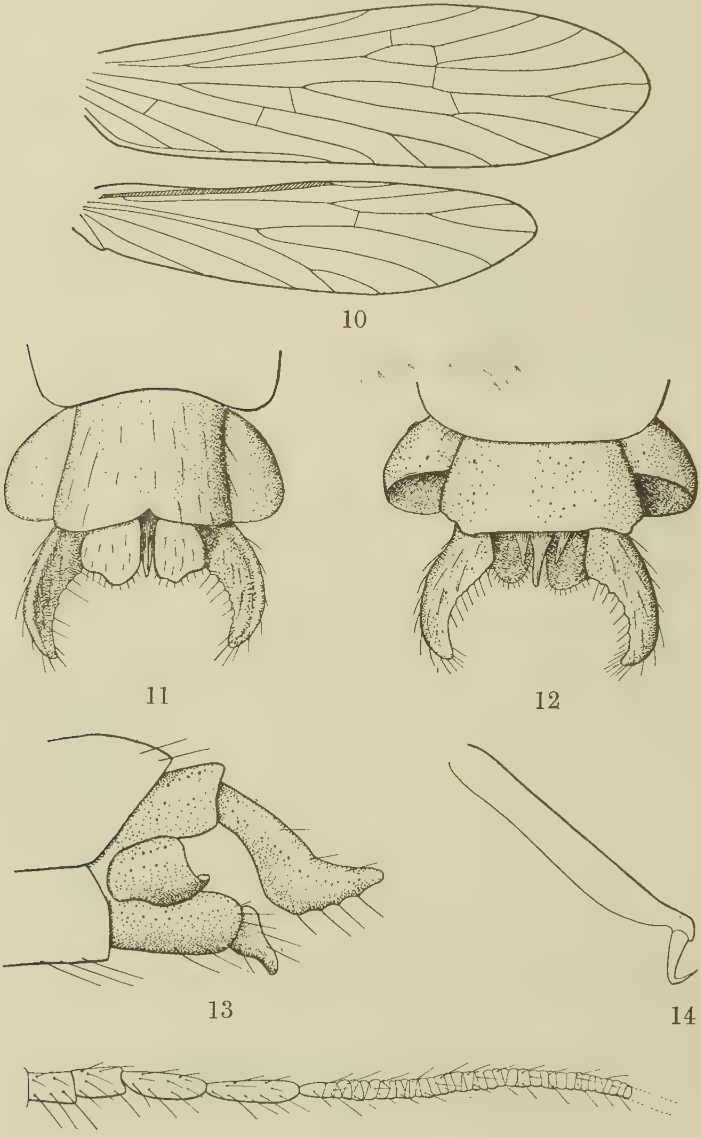
Figs. 6–9.—*Chimarrha intexta*, sp. n. ♂. 6, genitalia dorsal; 7, inferior appendages, internal view; 8, genitalia lateral; 9, wings.

Length of anterior wing, 4 mm.

Sierra Leone, Njala, 21.viii.1930 (*E. Hargreaves*).
Type ♂ is a balsam preparation in the British Museum collection.

Psychomyiellodes, gen. nov. (Psychomyidae).

The single known species has the general appearance of a small, darkish *Psychomyia*. The genus is closely allied to *Psychomyiellina*, but in the posterior wings there is no projecting angle along the costal margin. First and second joints of the maxillary palpi short and equal to each other; third and fourth joints each about twice as long as the first joint; fifth joint longer than the others put together (broken in the single example before me). Ocelli absent. Spurs 2.4.4, the inner apical spur of the posterior leg abnormally formed with a stout basal portion terminating in a short round-turned claw. Anterior wings with forks 2, 3, 4 and 5; discoidal and median cells closed; a cross-vein uniting the radial sector with the radius; wing rather narrow, apex rounded. In the posterior wing, the sub-costa and radius are fused, only forks 2 and 5 are present; discoidal and median cells wanting; wing rather narrow with no projecting angle along the costal margin; apex sub-acute.



FIGS. 10–15.—*Psychomyiellodes ungulata*, sp. n. ♂. 10, wings; 11, genitalia ventral; 12, dorsal; 13, lateral; 14, specialised spur of ♂ posterior leg; 15, maxillary palpus.

Type species *P. ungulata*, sp. n.

Psychomyiellodes ungulata, sp. n. Figs. 10–15.

The general features have been detailed under the generic description.

Male genitalia : margin of last dorsal segment straight; superior appendages from above, long, curving towards each other with concave inner margins furnished with strong spines, rather more numerous towards the apices; from the side, directed slightly downward, base rather narrow, lower margin convex towards the centre, apex directed backward. There is a pair of appendages or rounded plates, possibly representing intermediate appendages directed strongly outwards so that, from above, they extend far outside the dorsal segment, outer margins curved; from behind, they have the appearance of cups; from the side, the lower margin is slightly sinuous and projects beyond the upper. Penis, broad at base narrowing to an acute apex. There is a lightly chitinised upper penis cover showing from above and behind as a pair of pointed processes. Inferior appendages from beneath, short and broad, apices broad and sinuate; from the side, broad at base, directed downward and narrowing to finger-like apices. The last sternite from beneath, quadrangular with margin slightly excised; from the side, it appears as a rather narrow, rectangular projection.

Length of anterior wing, ♂, 3 mm. ♀ unknown.

SIERRA LEONE, Njala, x.1928 (*E. Hargreaves*).
Type ♂ is a balsam preparation in the British Museum collection.

Setodes squamosa, sp. n. Figs. 16–21.

Head silvery white at the vertex with shades of greenish-yellow round the oculi; hairs clothing the head, white; palpi ochraceous; antennae, basal joint pale ochraceous, remainder slightly darker.

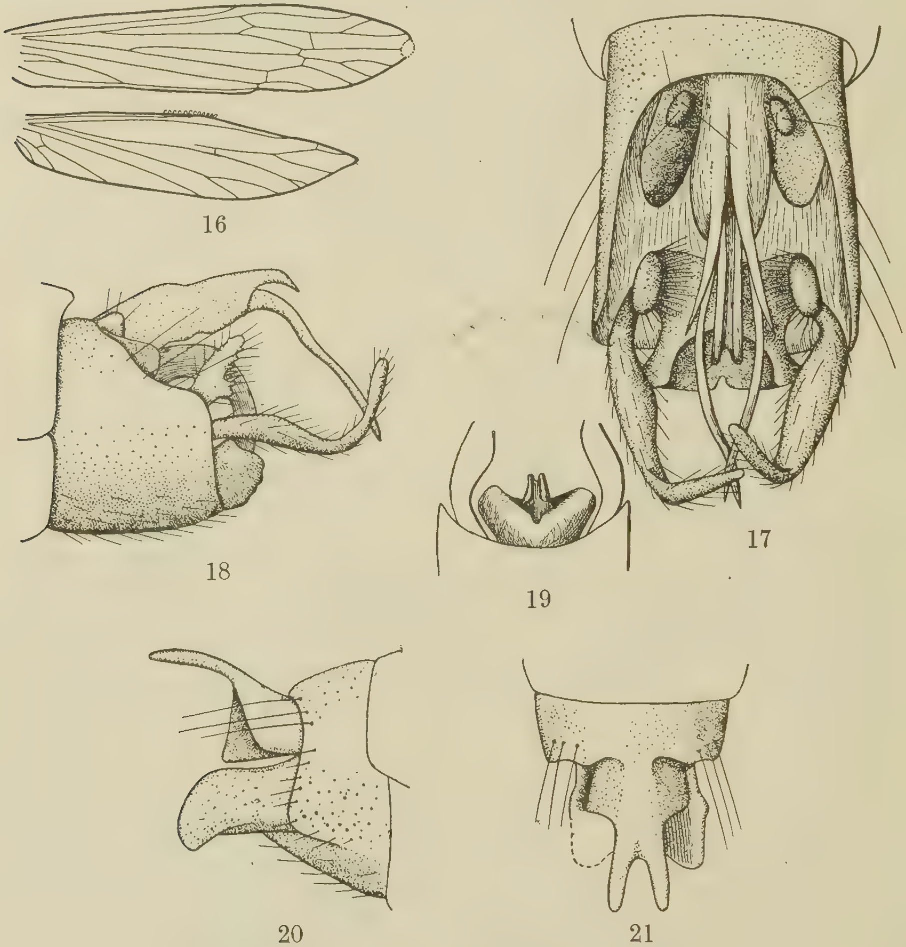
Wings : anterior, over the greater area, clothed with yellowish-green hairs; along the post-costal area is a band of white scales along which are eight or nine dark spots formed by clusters of chocolate-brown scales. The apical third of the wing bears a broad U-shaped marking, caused by the presence of a dense mass of chocolate-brown scales amidst which are small patches of white scales; there are a few isolated spots made by brown scales in the apical cellules. Posterior wings hyaline, the sector being broken and wanting towards the base as in *viridis.*

Legs pale ochraceous.

Abdomen ochraceous above, paler beneath.

Male genitalia : margin of last dorsal segment from above, widely excised; proceeding from the centre of the excision is a long, strongly chitinised process, no doubt an upper penis cover, which divides into two slender sinuous spines directed backward and downward; towards the base of this process, on its upper surface, arises a pair of much shorter, stouter spines which, seen from the side are rather stout at the base, curving backward and downward and terminating in acute points; from above, the margins of these upper spines are seen to extend towards the base of the process. The whole process, from the side, is very stout at the base for nearly half its length, with the upper and lower margins sinuous : from above, on each side of this process are two small superior appendages, oval in shape with small callosities on the upper surfaces at the base; from the side they are directed downward and are seen to be twisted, causing the outer margins to appear rectangularly excised. Penis arching strongly downward. Inferior appendages branched; the main branch is long and slender with apical portion abruptly upturned; at the base is a small upper branch with a very irregular, serrated margin, fringed with strong hairs; arising also from the base is a lower branch; the lowest branches of each appendage together form a deep cup in which the apex of the penis appears to rest. Seen from beneath, the cup is broad at the base, outer margins sloping outward; apex widely and deeply excised. The apex of the penis appears in the centre of the excision, and it may be seen that there is a deep channel running along its upper surface with sides standing up in narrow ridges.

Female genitalia : the genitalia are rather complicated; anal parts yellowish; the terminal dorsal segment is produced to form a stout fork which arises from a broad somewhat quadrilateral base. From the side the base is broad and is produced along its upper margin appearing as a slender, finger-like process, the lower margin being produced about midway in a downward and somewhat backwardly directed angle; a sinuous ridge divides the base of this angle from the upper part of the process. Below the fork are two broad, rounded plates, one of which in the single ♀ before me is broken off.



Figs. 16–21.—*Setodes squamosa*, sp. n. ♂. 17, genitalia dorsal; 18, lateral; 19, ventral process and bases of inferior appendages. ♀. 16, wings; 20, genitalia lateral; 21, dorsal.

Length of anterior wing, ♂, 6·5 mm.
Length of anterior wing, ♀, 5·5 mm.

NATAL, Weenen, x.1927 (*H. P. Thomasset*).
Type ♂ and paratype ♀ in the British Museum collection.

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